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REVIEW OF GEOGRAPHICAL STOCKS OF TROPICAL DOLPHINS (*Stenella* spp. and *Delphinus delphis*) IN THE EASTERN PACIFIC

by

William F. Perrin, Michael D. Scott,
G. Jay Walker, and Virginia L. Cass

ADMINISTRATIVE REPORT LJ-84-02

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REVIEW OF GEOGRAPHICAL STOCKS OF TROPICAL DOLPHINS (*STENELLA* SPP. AND *DELPHINUS DELPHIS*) IN THE EASTERN PACIFIC

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January 1984

Administrative Report LJ-84-02

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ABSTRACT

Information on geographical variation is reviewed for *Stenella attenuata*, *S. longirostris*, *S. coeruleoalba*, and *Delphinus delphis* in the eastern tropical Pacific, and boundaries for potential management units are proposed. National Marine Fisheries Service and Inter-American Tropical Tuna Commission sighting records made from 1979-1983 which were outside the 1979 SOPS boundaries were examined for validity. Tagging returns and morphological data were also analyzed. Several stock ranges are expanded or combined. Three management units are proposed for *S. attenuata*: the coastal, northern offshore, and southern offshore spotted dolphins. Four management units are proposed for *S. longirostris*: the Costa Rican, eastern, northern whitebelly, and southern whitebelly spinner dolphins. Two provisional management units are proposed for *S. coeruleoalba*: the northern and southern striped dolphins. Five management units (two of which are provisional) are proposed for *D. delphis*: the Baja neritic, northern, central, southern, and Guerrero common dolphins. Division into management units was based on morphological stock differences and distributional breaks. Several definitions of population units used for management purpose are discussed.

INTRODUCTION

Tuna fishermen make use of four species of dolphins in the international purse-seine fishery for yellowfin tuna in the eastern tropical Pacific, in finding and capturing the tuna (Smith 1983). These are (in order of importance to the fishery) the spotted dolphin, *Stenella attenuata*; the spinner dolphin, *S. longirostris*; the common dolphin, *Delphinus delphis* and the striped dolphin, *S. coeruleoalba*. Perrin, Scott, Walker, Ralston and Au (1983) delineated the known ranges of the species in the eastern Pacific in a

recent review. The purpose of this paper is to review available information on geographical variation of the four species in the eastern Pacific and to propose boundaries for potential management units.

Geographical variation in S. attenuata and S. longirostris was first described by Perrin (1972b, 1975a). He placed the nominal endemic S. graffmani (Lonnberg 1934) (described from Acapulco, Mexico) in the synonymy of S. attenuata (Gray 1846) and described three subspecies from the eastern and central Pacific: 1) the coastal spotted dolphin, S. a. graffmani (formerly S. graffmani), a relatively large and heavily spotted form thought to occur within about 20-25 km of the shore and in gulfs and embayments from southern Mexico to Colombia; 2) the offshore spotted dolphin, S. a. subsp. "A" (unnamed), a smaller and more lightly spotted pelagic form thought to occur from about 25 km offshore from Cabo San Lucas, Mexico to Colombia and west to at least 145°W longitude in tropical waters; and 3) the Hawaiian spotted dolphin, S. a. subsp. "B" (unnamed) from Hawaiian waters, similar to the offshore form but less spotted and with a larger skull. In the case of the spinner dolphins, specimens from the eastern tropical Pacific had been referred (by Hester, Hunter and Whitney, 1963) to S. microps (Gray 1846; described from an unknown locality) and animals from Hawaii referred (by Morris and Mowbray 1966) to S. roseiventris (Wagner 1846; described from the western Pacific). Perrin (1975a) considered the spinner dolphins to belong to a single species, S. longirostris (Gray 1848) (described from an unknown locality) and described four subspecies. The Costa Rican spinner dolphin, S. l. subsp. "A" (unnamed), is a relatively long and slender form of overall gray color and with a very long rostrum, from nearshore waters of Costa Rica and El Salvador. The eastern Pacific spinner dolphin, S. l. subsp. "B" (unnamed; formerly identified as S. microps), is a smaller but similarly colored form with a small skull and (in many adult males) with the dorsal fin canted forward almost so as to appear reversed and occurs westward from the coast of Mexico west out to about 800 km. The whitebelly spinner dolphin (so called by tuna fishermen), S. l. subsp. "C" (unnamed), is similar to the eastern spinner dolphin in size and skull but has a ventrolateral white area extending from the flipper to the genital region and a less triangular dorsal fin; it ranges from about 800 km offshore to 140°W longitude. The Hawaiian spinner dolphin, S. l. subsp. "D" (unnamed; formerly identified as S. roseiventris), is a relatively large form with large skull, sharply defined three-part color pattern and slightly falcate dorsal fin, and occurs in Hawaiian waters. The first and last of these forms ("A" and "D") were at that time each known from only a few specimens, as were the coastal and Hawaiian forms of the spotted dolphin. Perrin (1972a) described geographical variation in the color pattern of S. longirostris in detail and proposed a generalized model for variation in this and other delphinids. Under this scheme, the variation in the spinner dolphin is seen as variation in extent and density of a color-pattern component called the "dorsal overlay," with the overlay being modally darkest and most extensive in the Costa Rican and eastern forms and lightest and least extensive in the Hawaiian form. The color patterns of the various forms are thus perceived as variations on a theme rather than as discretely different patterns.

As more distributional data have accumulated, the known ranges of the several forms of S. attenuata and S. longirostris have expanded (Perrin 1975b; Perrin, Smith and Sakagawa 1976, 1982; SWFC 1976). Studies of material from

below the equator led to division of the offshore spotted dolphin and the whitebelly spinner dolphin each into northern and southern stocks by Perrin, Sloan and Henderson (1979). They found the southern offshore spotted dolphin to be slightly smaller than the northern animal, with a larger skull and more distinct color pattern. The southern whitebelly spinner dolphin they found to be larger than the northern form, with coloration more resembling that of the Hawaiian form. These findings and additional distribution records were taken into account in the most recent delineation of the ranges, by Au, Perryman and Perrin (1979), which was used in an exercise referred to below as "SOPS 1979" for Status of Porpoise Stocks [Workshop], 1979) in 1979 (Smith 1979, 1983) (Figures 1 and 2). Scott (1981) and Alverson (1980, 1981) reviewed the ranges, the former incorporating data through 1980.

The range of S. coeruleoalba in the eastern Pacific was first divided into subareas in a 1976 stock assessment exercise (SWFC 1976). The partition into "northern," "north equatorial" and "south equatorial" management units was based solely on apparent latitudinal gaps in distribution. The division was modified slightly in 1979 (Au et al. 1979; Smith 1979, 1983), again on distributional grounds alone, yielding five units: "northern temperate," "northern tropical," "central tropical," "southern tropical" and "southern temperate" (Figure 3). To date, geographical variation in this species in the eastern Pacific has not been studied.

Delphinus delphis varies morphologically a great deal in the eastern Pacific. Banks and Brownell (1969) referred a short-beaked offshore form and a long-beaked neritic form occurring off southern California and Baja California to D. delphis L. and D. bairdii Dall 1873, respectively. Van Bree and Purves (1972) reported material that showed intergradation in skull morphology between the two forms and concluded that they belong to the single species D. delphis. Evans (1975, 1976a and b, 1983) described five forms in the eastern Pacific: 1) a relatively large form inhabiting waters inside the 100-fathom curve off southern California and Baja California, with a very long rostrum and a muted color pattern (later called the "Baja neritic" form); 2) and 3) small, short-beaked northern temperate and northern tropical forms; and 4) and 5) large short-beaked central and southern tropical forms delineated by apparent latitudinal gaps in distribution. He also suggested the possible existence of an "equatorial- oceanic" population inhabiting waters west of 95°W longitude. These stock divisions were used in the 1976 stock assessment (SWFC 1976). On the basis of additional distribution data, Au et al. (1979) modified the boundaries of the stocks and added a "southern temperate" stock (Figure 4). They included all animals between 3° and 15°N latitude in the "central tropical" stock, not recognizing Evans' tentative "equatorial-oceanic" stock. In the 1979 stock assessment (Smith 1979 and 1983), the Baja neritic and northern temperate stocks were combined into a single management unit. The stock structure of D. delphis was most recently reviewed by Scott (1981).

In this paper we review developments and data collected for the four species since the 1979 stock assessment, including the results of analyses carried out under contract to the Southwest Fisheries Center by the University of Oklahoma (Schnell, Douglas and Hough 1982). Definitions of terms are discussed in Appendix 1.

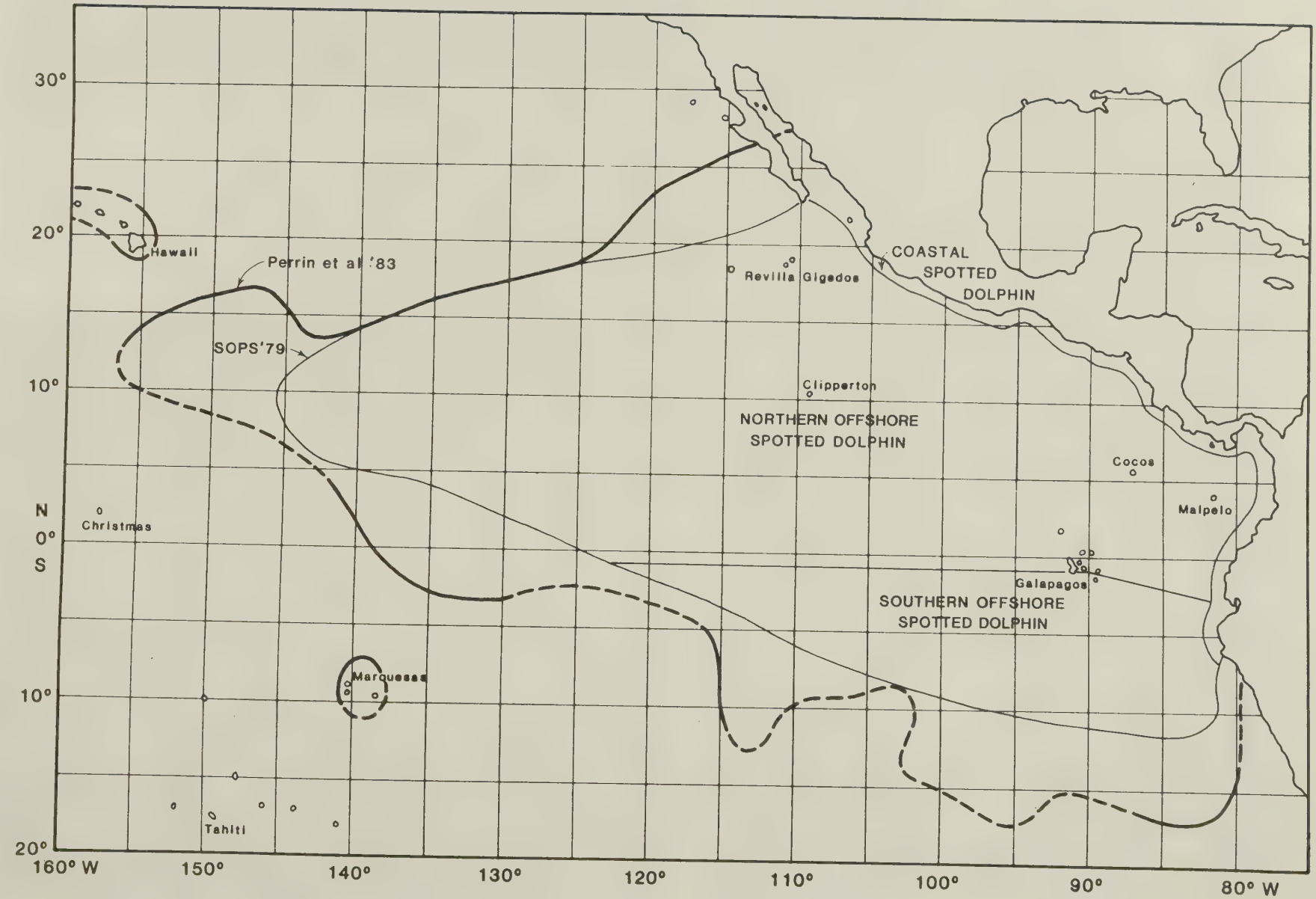

Figure 1. Known distribution of S. attenuata in the eastern Pacific, showing SOPS '79 species range and stock boundaries, and new species range (from Perrin et al. 1983).

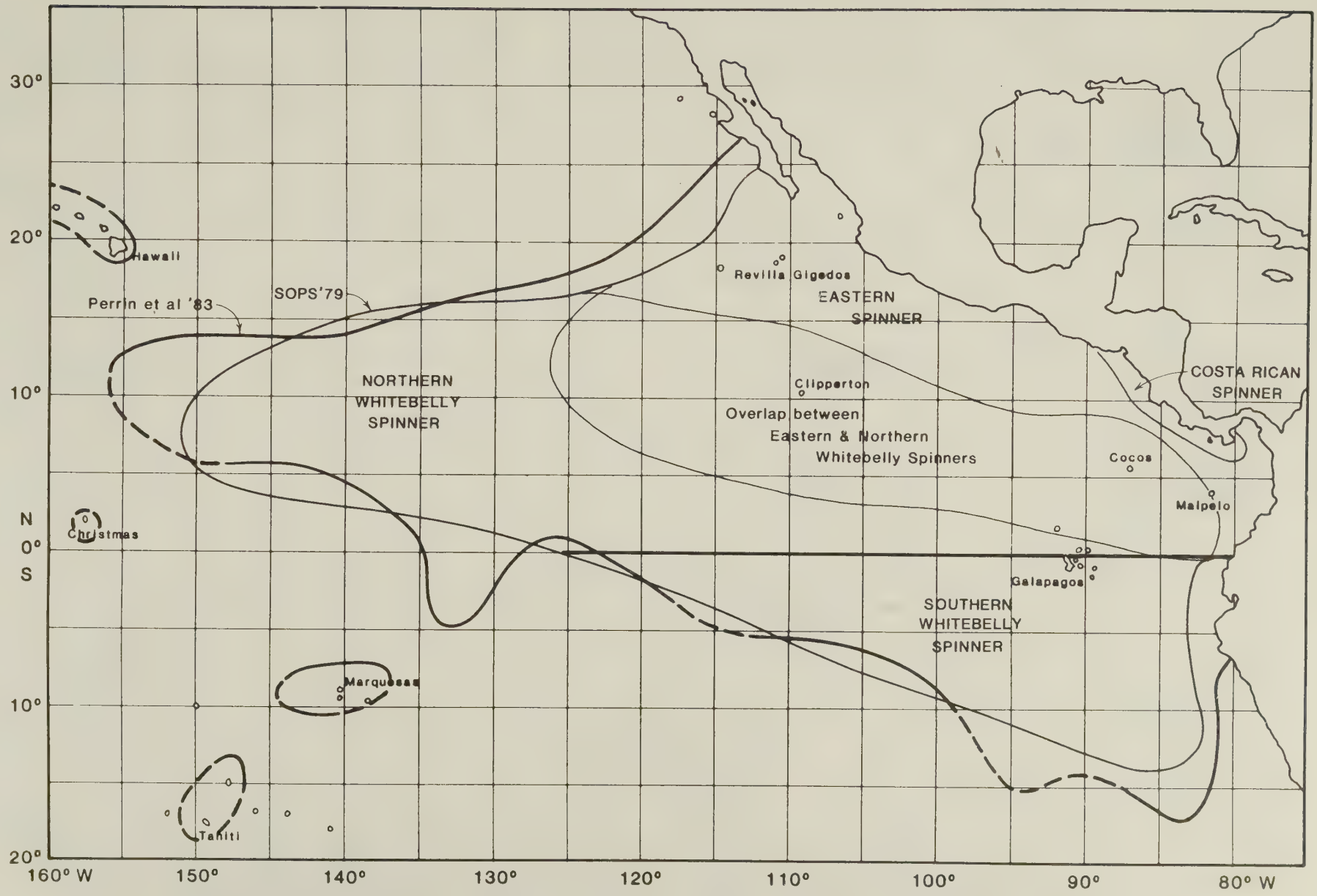

Figure 2. Known distribution of S. longirostris in the eastern Pacific, showing SOPS '79 species range and stock boundaries and new known species range (from Perrin et al. 1983).

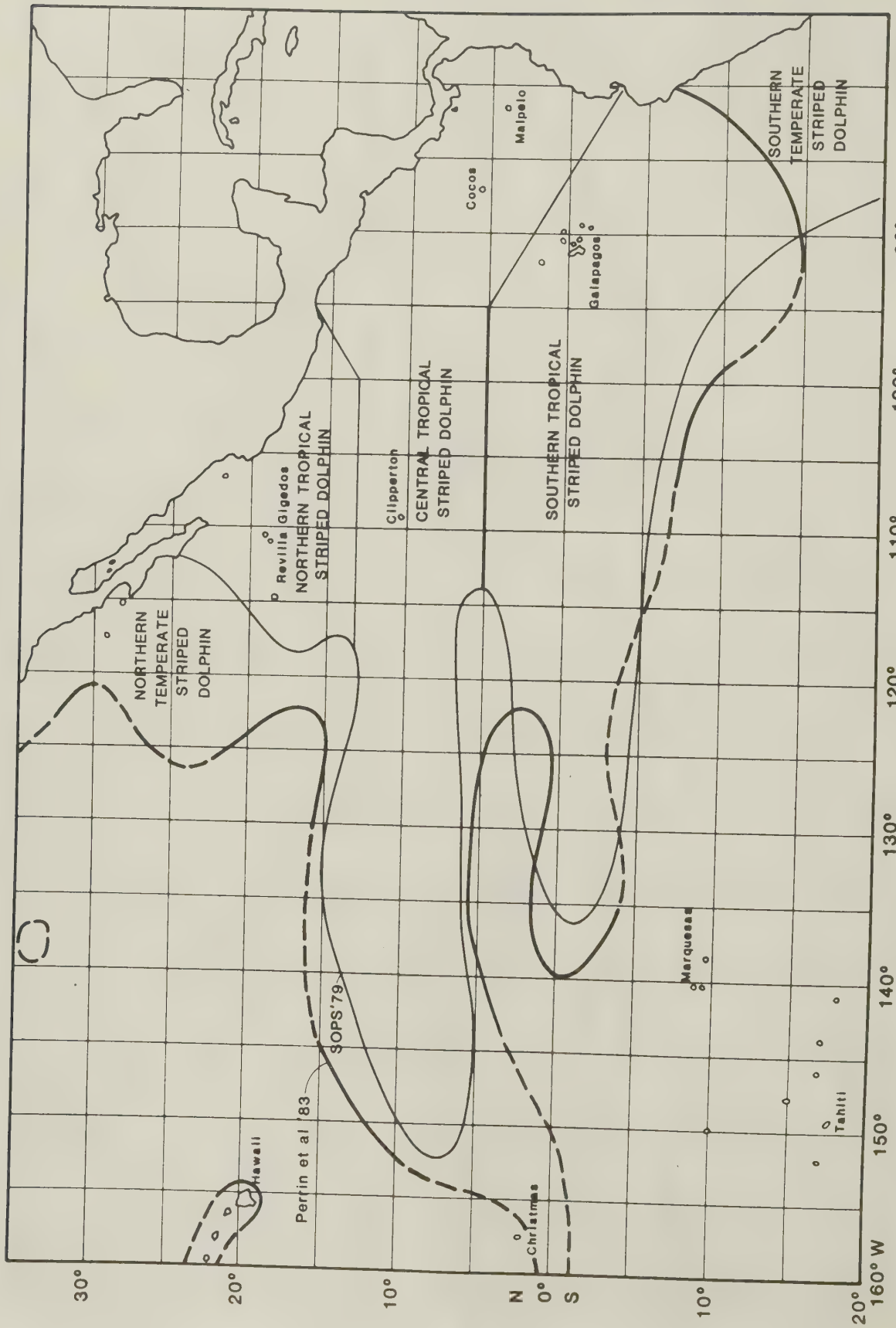

Figure 3. Known distribution of S. coeruleoalba in the eastern Pacific, showing SOPS '79 boundaries and new species range (from Perrin et al. 1983).

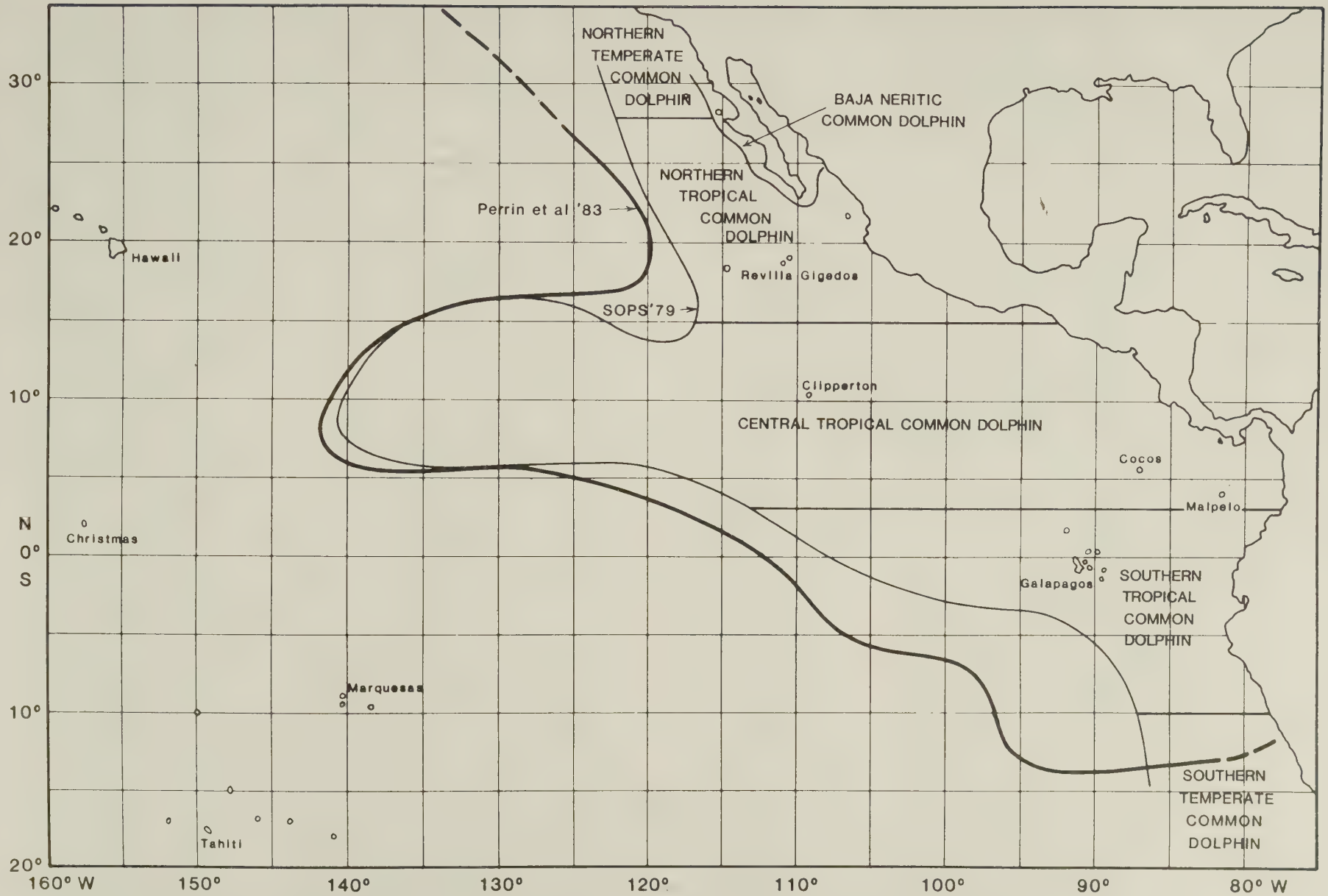

Figure 4. Known distribution of Delphinus delphis in the eastern tropical Pacific, showing SOPS '79 species range and stock boundaries and new known species range (from Perrin et al. 1983).

MATERIALS AND METHODS

Morphological Analyses

The samples and methods used in the contracted analyses of variation in skull and body length in S. attenuata and S. longirostris are described in Schnell et al. (1982). In addition to consideration of the results obtained by those authors, we reviewed all body-length data collected through 1981 (Figures 5-8), including some data for the inshore forms of S. attenuata and S. longirostris not included in the contracted analyses, and data for S. coeruleoalba and D. delphis. We also examined data on frequencies of ovarian corpora for S. attenuata and S. longirostris. Sources of the data are described in Perrin and Oliver (1982); statistical reporting areas are defined in Appendix 2. Computerized processing and analysis of these data (and the distribution data) are described in Appendix 3.

Distribution data

The sources and nature of the distribution data are described in Perrin et al. 1983. Data were included for all NMFS and IATTC tuna/dolphin observer cruises from 1979 through most of 1983.

S. attenuata

We reviewed all records of spotted dolphins from within 100 nautical miles of the coast (or a coastal island) that were identified to stock (coastal or offshore). These comprised 1650 sightings and collection records. Of 502 coastal records, we concurred with the identifications for 218; 67 were changed to offshore, and 217 were downgraded to unidentified spotted dolphin. Of 1147 offshore records, we accepted 456, changed 44 to coastal, 640 to unidentified spotted and 7 to unidentified dolphin. The large number of changes to unidentified spotted was occasioned by the fact that in recent years NMFS observers aboard commercial purse seiners have largely identified spotted dolphins to stock based only on locality without regard to morphological information, all those within 50 nm of the coast being designated as coastal and all those outside 50 nm as offshore. In point of fact, the coastal form was described on the basis of skull characters, body size and coloration (Perrin 1975a).

In reviewing a sighting, we considered the morphological observations recorded by the observer and any photographs, body-length data, life history data, and osteological specimens collected in association with the sighting. If the observer noted that the animals seemed larger and/or more heavily spotted than those seen far offshore, or, better, if the photos, length data or specimens indicated this (based on the published information for the two forms), we considered the record to be a confirmed record of the coastal form. Because the question is one of modal differences between forms within a species, the identification was judgmental in many cases, especially if only a

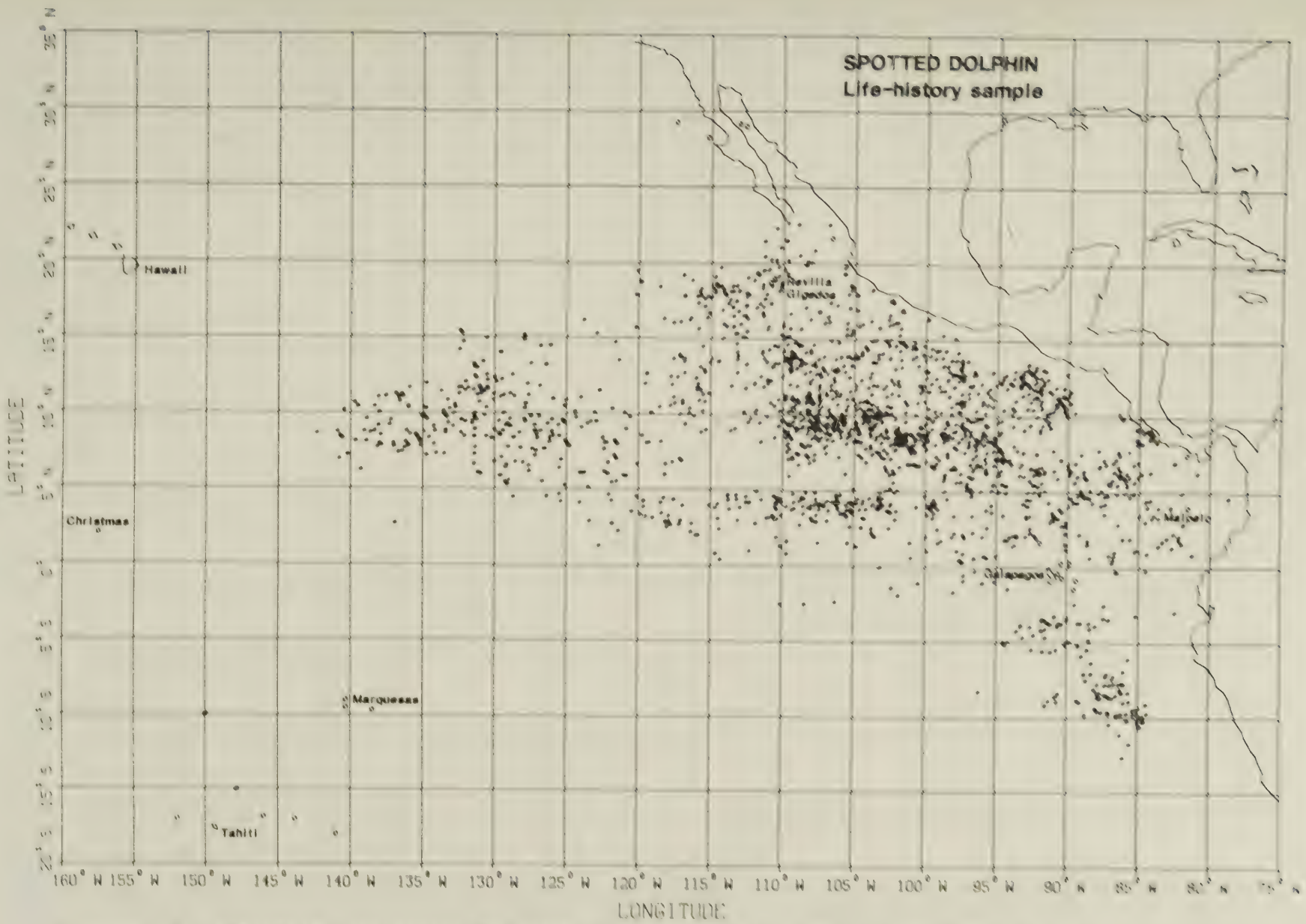

Figure 5. Collection localities for adult specimens of S. attenuata included in body-length analyses. Adults defined as males with testis-epididymis weight of 100 gm or more and females with at least one ovarian corpus. Open dots are small islands.

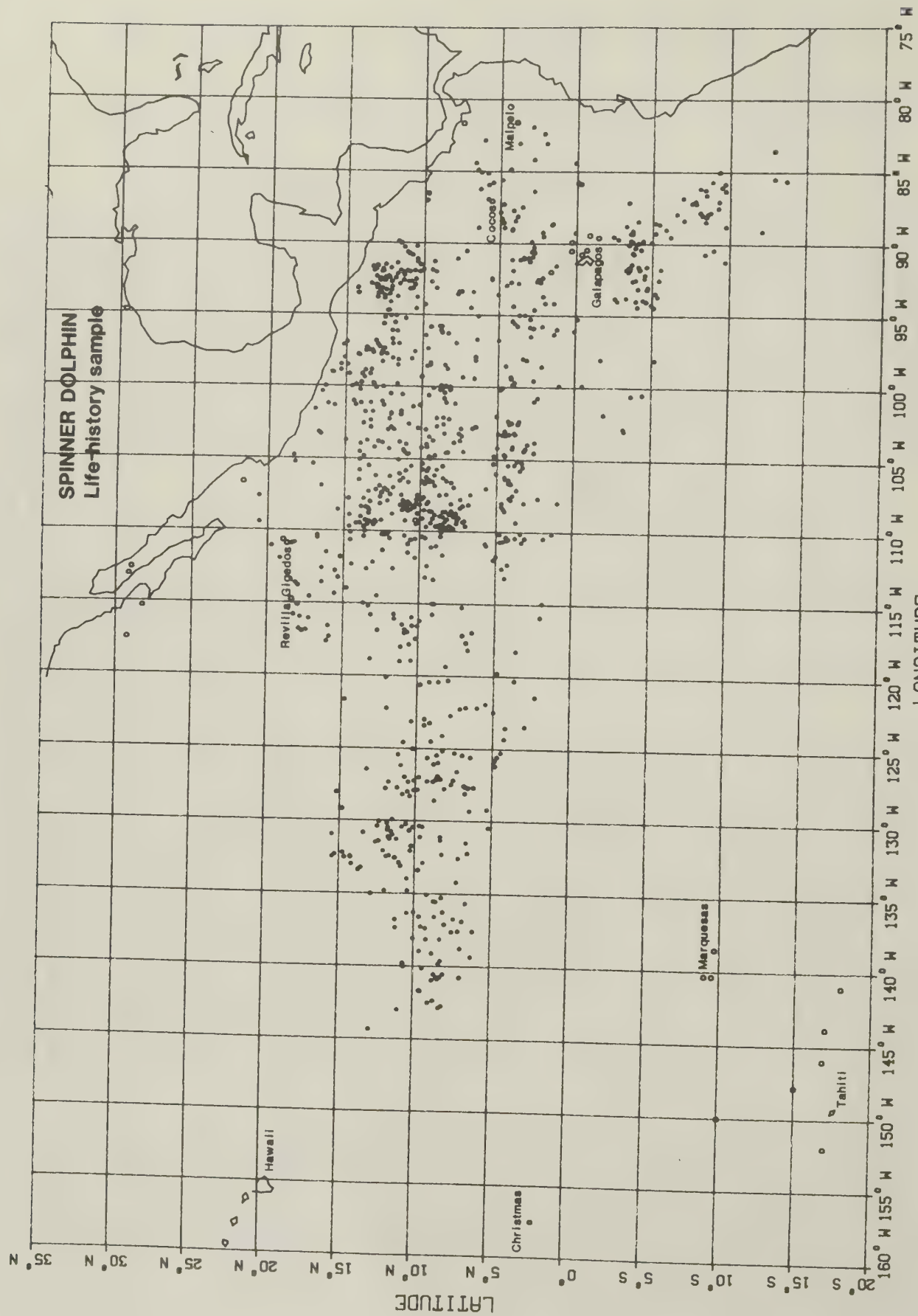

Figure 6. Collection localities for adult specimens of S. longirostris included in body-length analyses. Adults defined as for S. attenuata. Specimens not identified to stock are not included.

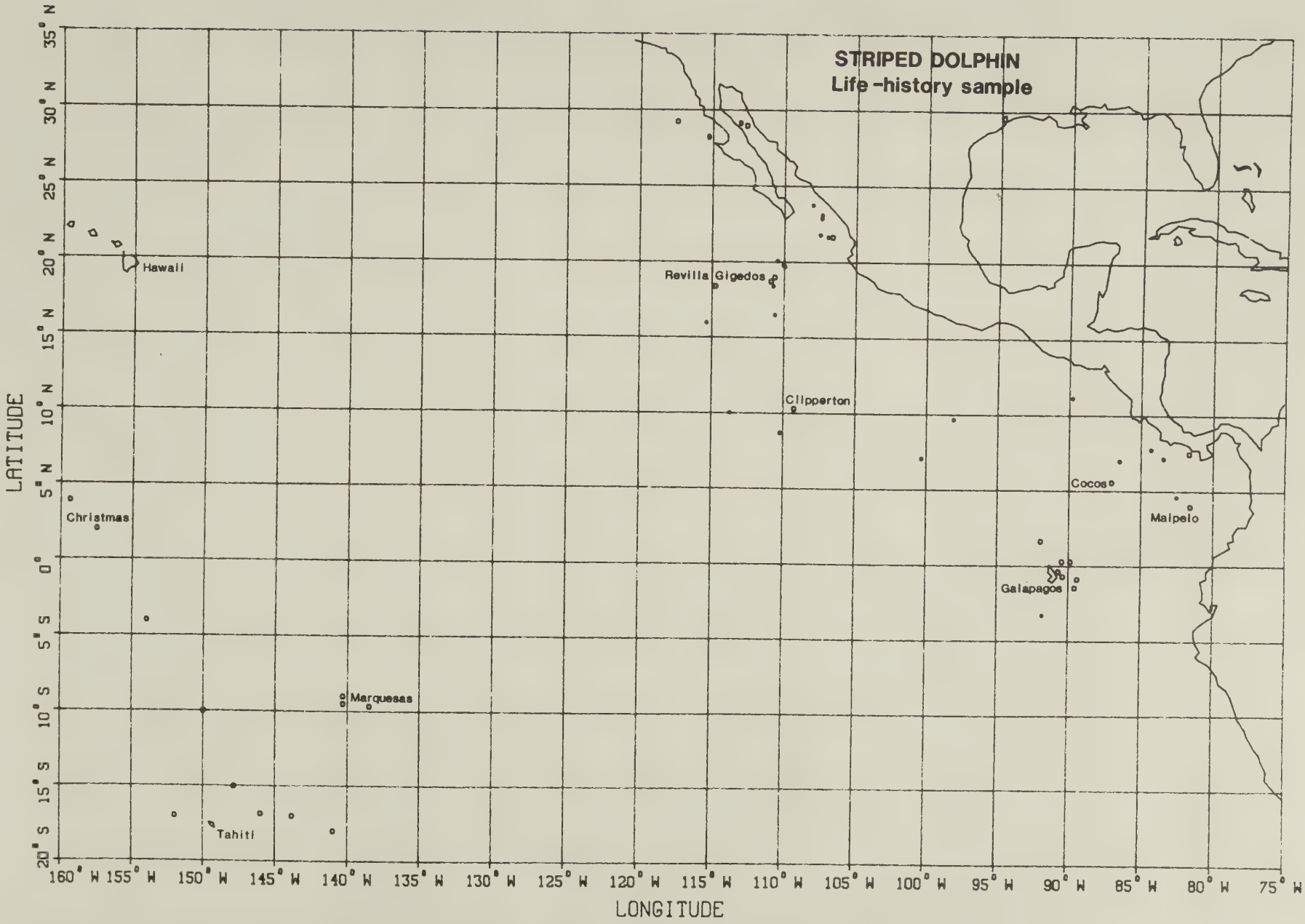

Figure 7. Collection localities for adult specimens of S. coeruleoalba included in body-length analyses. Adults defined as for S. attenuata.

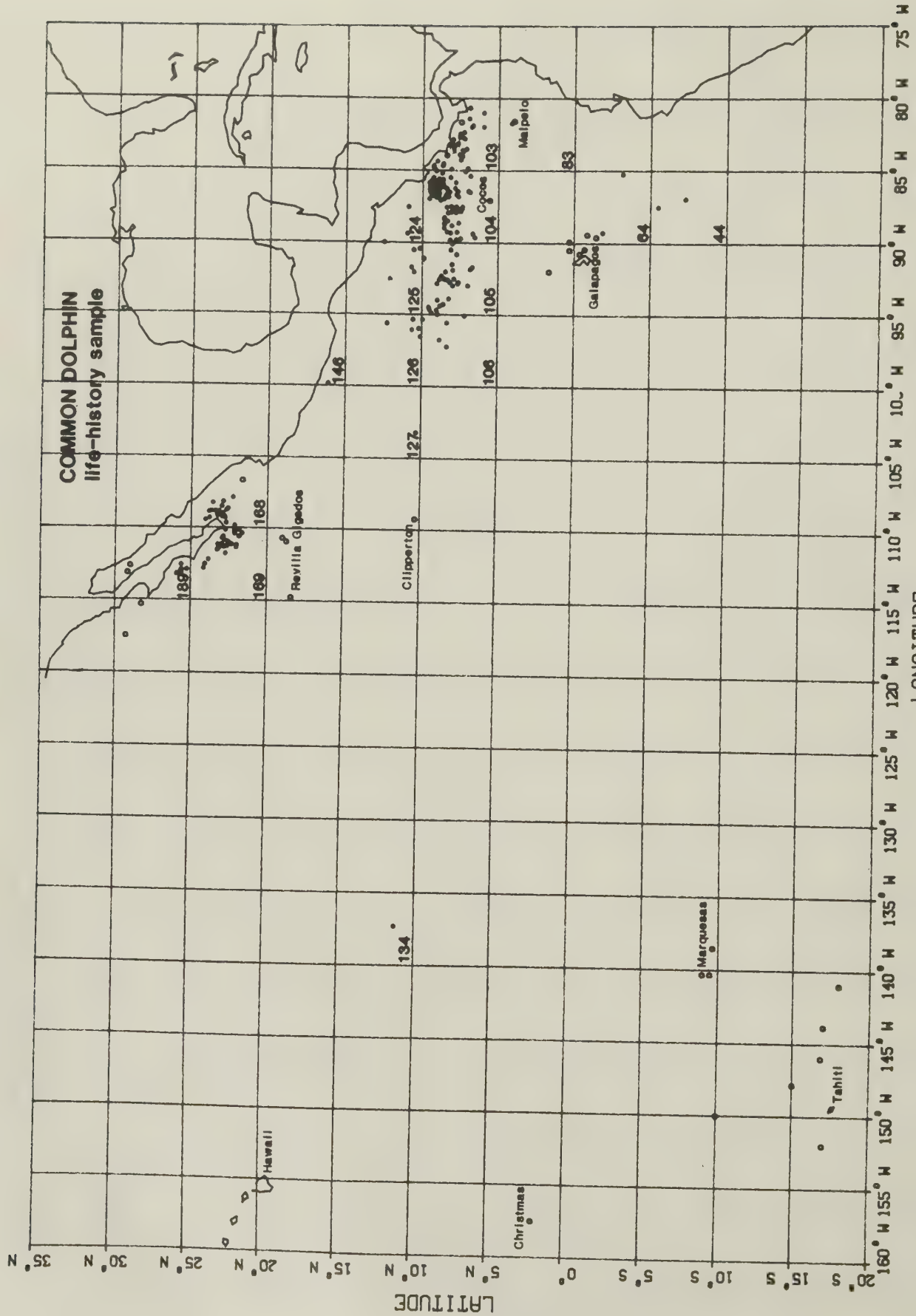

Figure 8. Collection localities for adult specimens of Delphinus delphis included in body-length analyses. Adults defined as for S. attenuata. See Appendix 2 for square numbering guide.

few animals were measured or if the observer's recorded comments were sketchy or ambiguous and voucher data and specimens were absent. We tried to err on the side of conservatism, relegating the more weakly supported sightings to the unidentified category, but undoubtedly we classified some sightings of the coastal form as offshore and vice versa.

In evaluating the observer's recorded information, we also considered such factors as sighting distance and conditions, experience of the observer, and quality of documentation and identifications for other sightings made by the same observer. In addition, we considered the context of the sighting record. If, for example, one net set (a sighting record) was made on the same school or near the same time and in the same area as a previous set assignable to stock based on recorded observations or specimens, we considered the second record to be of the same form.

S. longirostris

To examine the distribution of the Costa Rican spinner, we reviewed all records of S. longirostris within 50 nm of the coast. The number of confirmable records was small, mainly because the Costa Rican form differs externally from the eastern form only in total body length and relative length of the rostrum and apparently not in coloration. Also, the Costa Rican spinner dolphin is only very rarely captured by the tuna fishermen (Perrin 1975b). Of 42 Costa Rican records, we confirmed 33, assigning the rest to unidentified spinner. Of these confirmed records, 24 were based on aerial photographs taken during a photogrammetric experiment by the Inter-American Tropical Tuna Commission in 1980. One of 196 eastern records was judged to be Costa Rican; 28 were confirmed as eastern and 157 changed to unidentified spinner. One of 118 unidentified records was changed to eastern.

We also reviewed all records of eastern spinner dolphins and whitebelly spinner dolphins outside the respective SOPS '79 boundaries (see Figure 2). We again adopted a conservative stance because of the necessarily judgemental nature of the identifications in many cases. Of 198 eastern records, we confirmed 115 (8 supported by specimen data), assigned 40 to whitebelly, 41 to unidentified spinner, and two to S. attenuata. Of 280 outlying whitebelly records, 184 were confirmed (one with specimen data), 35 assigned to eastern, 49 to unidentified spinner, one to S. attenuata, one to Delphinus delphis, and 10 to unidentified dolphin.

In addition to considering the sighting factors discussed above, we found it necessary to "second-guess" the observer's understanding of the modal nature of the differences between the two forms, as a large number of sightings of "mixed" schools of eastern and whitebelly spinner dolphins were reported. In some cases, this designation was likely valid, because the observer noted separate groups of the two forms in the net. In other cases we assigned the "mixed" sighting to one or the other of the two forms because only a very few individuals of the "other" type were seen, as would be expected in the case of subspecific-level modal difference. There were a large number of "mixed" sightings, however, where it was unclear from the information recorded if the record should be assigned to both forms. In some

cases, color-pattern "intergrades" were reported, again something to be expected in the case of subspecific variation but difficult to evaluate when assigning a school to one mode or the other or both. In these situations, we made judgmental decisions based on other aspects of the sightings, giving heavy weight to the experience and apparent knowledgability of the observer.

We noted three additional problems primarily encountered in sightings made by inexperienced observers, usually during the first few days of a first cruise:

1) Juvenile eastern spinner dolphins appear whitebelly-like in having a light ventrum (Perrin 1972a), and some were clearly misidentified in the sighting records. Where specimens were collected, we were able to detect the error; other instances probably remain in the whitebelly spinner dolphin records that we accepted.

2) Adult eastern spinner dolphins when seen at a distance, especially when spinning, appear slightly lighter ventrally than dorsally. In some cases it was clear that the observer had not yet seen whitebelly spinners and was mistaking this muted counter-shading for the sharply demarcated dark-gray and white pattern of the whitebelly form. Again, some instances of this have probably gone undetected in our review.

3) New observers in some cases clearly confused the similar fishermen's terms "whitebelly" (Delphinus delphis, S. coeruleoalba or Lagenodelphis hosei) and "whitebelly spinner" (S. longirostris). In an earlier review of species ranges (Perrin et al. 1983) we found that this had led to obviously spurious records of S. longirostris far north of the tropical habitat. Again, in the present review we found sightings (made at a distance) which members of the crew identified as "whitebellies" but the inexperienced observer identified as "whitebelly spinners," most likely misunderstanding the crewman's identification.

In view of these difficulties, and because of the rather unusual broad overlap of the ranges of geographical forms (which usually, by definition, are allopatric but may not be in these highly mobile and socially complex cetaceans), we consider the allocation of outlying sightings to whitebelly and eastern spinners on balance to be less reliable than the allocations for the other stocks and species reviewed in this study.

Tagging

The tagging methods and operations (except for the tag releases listed in Table 1) have been described previously (Perrin, Holts and Evans, 1979; Jennings and Stives, 1979; Powers, Butler, Jennings, McLain, Peters and DeBeer, 1979; and White, Jennings, Gandy and Cornell, 1981). Part of the results (tag recapture and resights) were presented and analyzed in Perrin et al. (1979) and Jennings and Stives (1979).

Other Methods

Other methods investigated for potential use in delineating stocks are reviewed in Appendix 4.

Table 1. Releases of spaghetti tags (metal dart, type d -- Perrin, Holts and Evans 1979) by Mssrs. Martini and Nilson aboard the private vessel Serenity in 1975 and 1976. The species identifications are tentative.

Species	Tag No.	Date	Position
S. attenuata	05002	27DEC75	8° 20' N, 78° 45' W
" "	05004	"	8° 13' N, 78° 47' W
" "	05006	"	8° 08' N, 78° 50' W
" "	05007	"	8° 07' N, 78° 50' W
" "	05008	"	8° 06' N, 78° 50' W
" "	05017	"	8° 07' N, 78° 50' W
S. longirostris	05034	11MAR76	8° 23' S, 137° 36' W
" "	05036	12MAR76	8° 42' S, 139° 20' W
" "	05038	"	8° 42' S, 139° 40' W
" "	05040	20MAR76	8° 58' S, 140° 09' W
" "	05041	21MAR76	8° 57' S, 140° 03' W
" "	05043	"	8° 56' S, 140° 01' W
" "	05044	"	" "
" "	05046	22MAR76	8° 55' S, 140° 01' W
" "	05047	23MAR76	8° 57' W, 140° 06' W

Table 1. Continued.

Species	Tag No.	Date	Position
*Tursiops truncatus**	05009	3JAN76	0° 42' S, 89° 30' W
" "	05010	"	" "
" "	05011	"	0° 46' S, 89° 30' W
" "	05012	"	" "
" "	05013	"	" "
" "	05015	"	" "
" "	05019	"	" "
" "	05021	"	" "
" "	05025	22JAN76	1° 16' S, 90° 22' W
" "	05028	24JAN76	0° 50' S, 89° 41' W
" "	05030	5FEB76	0° 06' S, 90° 52' W
" "	05033	16FEB76	0° 38' S, 91° 33' W
Unidentified dolphin	05022	7JAN76	0° 48' S, 90° 11' W
(*T. truncatus* or	05029	24JAN76	0° 50' S, 89° 41' W
Delphinus delphis)	05031	16FEB76	0° 38' S, 91° 32' W

*Included here for completeness; these tagging data have not been published elsewhere.

SPECIES ACCOUNTS

S. attenuata

Our results for this species agree with those of similar earlier studies (Perrin 1975a and b; Perrin, Sloan and Henderson 1979) and the results of the multivariate analyses by Schnell et al. (1982). Our review of records within 100 nm of the coast confirmed the existence of a relatively large-bodied, heavily spotted form living near the coast from northern Mexico to Ecuador (Figure 9). The near-shore zone is not inhabited exclusively by the coastal form, however. There are well-supported records of the smaller, less-spotted offshore form within 20 nm of the coast, in close proximity to well supported records of the coastal form (Fig. 10A, B, C). Conversely, there are some well-supported records of the coastal form fairly well offshore, surrounded by records of the offshore form. The greatest distance from shore for a coastal record supported by body-length data was 70 nm (off central Mexico), and the supported offshore record closest to the coast was at 16 nm (also off central Mexico) (Figures 10 and 11). The transition from coastal to offshore is relatively regular out to about 60 nm, with a continuing low frequency of sightings of the coastal form out to 90 nm (Figure 11). The distance at which the number of included records east of the line which are offshore is equal to the number of coastal records excluded (offshore of the line) is about 35 nm. This, of course, is based on the distance-from-shore frequency distribution in the sample considered here. Within 50 nm, the boundary used in the past in stock assessment and management, the composition (based on the stratification in Figure 11) was 52.7% coastal and 47.3% offshore. A line drawn at 100 nm from shore could safely be said to encompass all of the coastal range.

The coastal form may also occur around some of the oceanic islands in the eastern Pacific (Revillagigedos, Clipperton Island, Cocos Island and Malpelo Island), but there is only one sighting record indicating this. An IATTC technician aboard a commercial seiner approximately 60 nm off Melpelo Island in 1983 observed a school of 15-30 robust and heavily-spotted dolphins that "looked like coastals." The distance from the mainland was approximately 240 nm. Without more records, it is difficult to say whether the observer just happened to see a few heavily-spotted offshore animals (which would be expected under the racial paradigm, given enough observation effort) or the animals around the Island are similar to those close to the mainland. We assume the former, pending availability of more information.

Adult male coastal spotted dolphins average about 23 cm larger than offshore males (those north of the SOPS '79 N/S boundary-- Fig. 1-- and east of 120°W longitude) and coastal females about 19 cm larger than offshore females (Figure 12), although there is broad overlap in length. The standard deviations for the coastal samples are appreciably larger than those for the offshore samples (CV = 5.07 and 3.91, respectively). This and the right-skew in the coastal female distribution may mean that some animals classified as coastal should have been identified as offshore, or that intergrades are more common in coastal schools than in offshore schools, i.e., that the coastal form is more variable, perhaps reflecting proportionately greater introgression of offshore genes into the coastal population than the

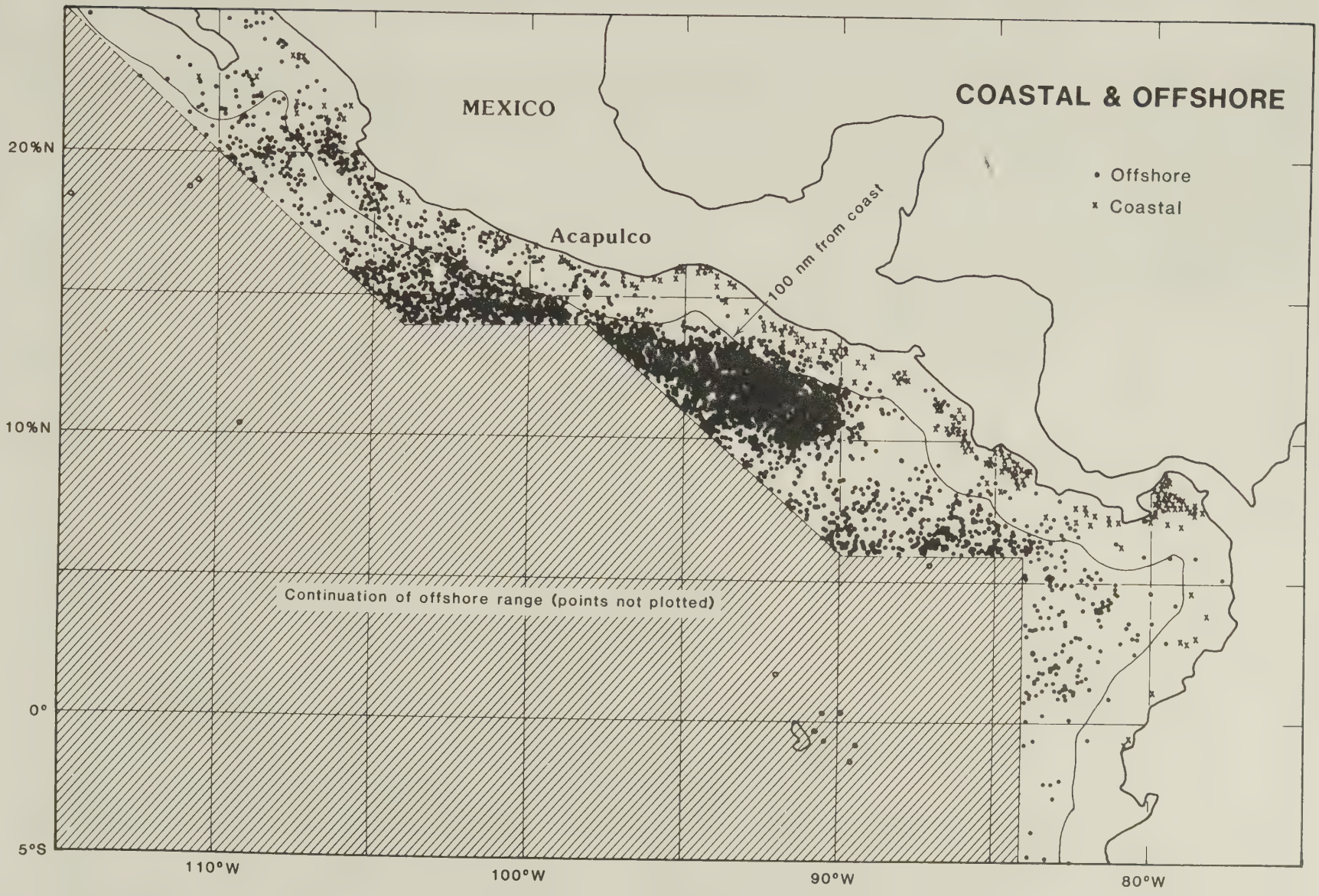

Figure 9. Records of offshore (dots) and coastal (circles) spotted dolphins in the far-eastern Pacific.

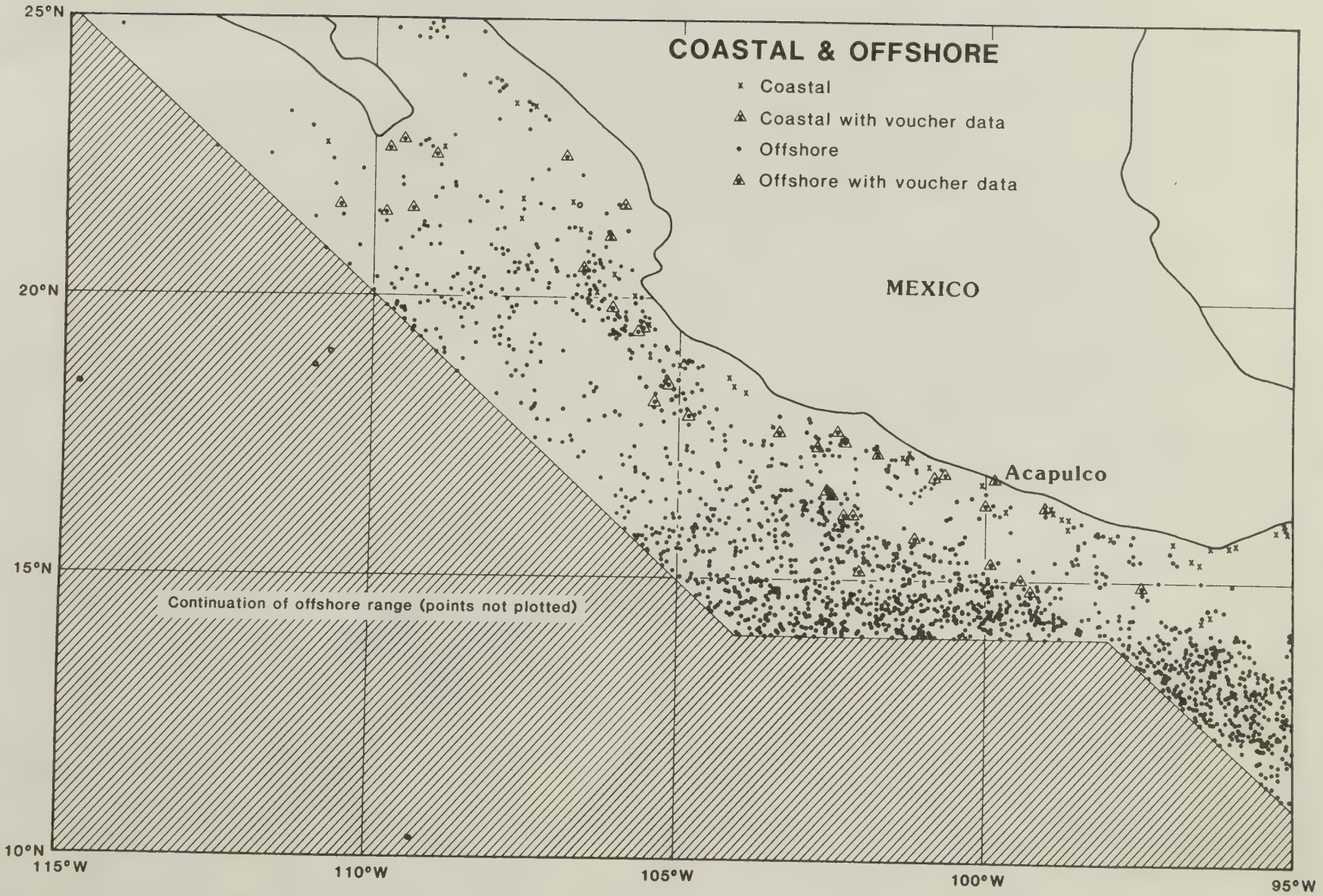

Figure 10. Records of offshore (small dots) and coastal spotted dolphins (large dots) off A) North America, B) Central America, and C) South America, with records that are supported by photos, measurements or osteological specimens indicated (triangles).

A

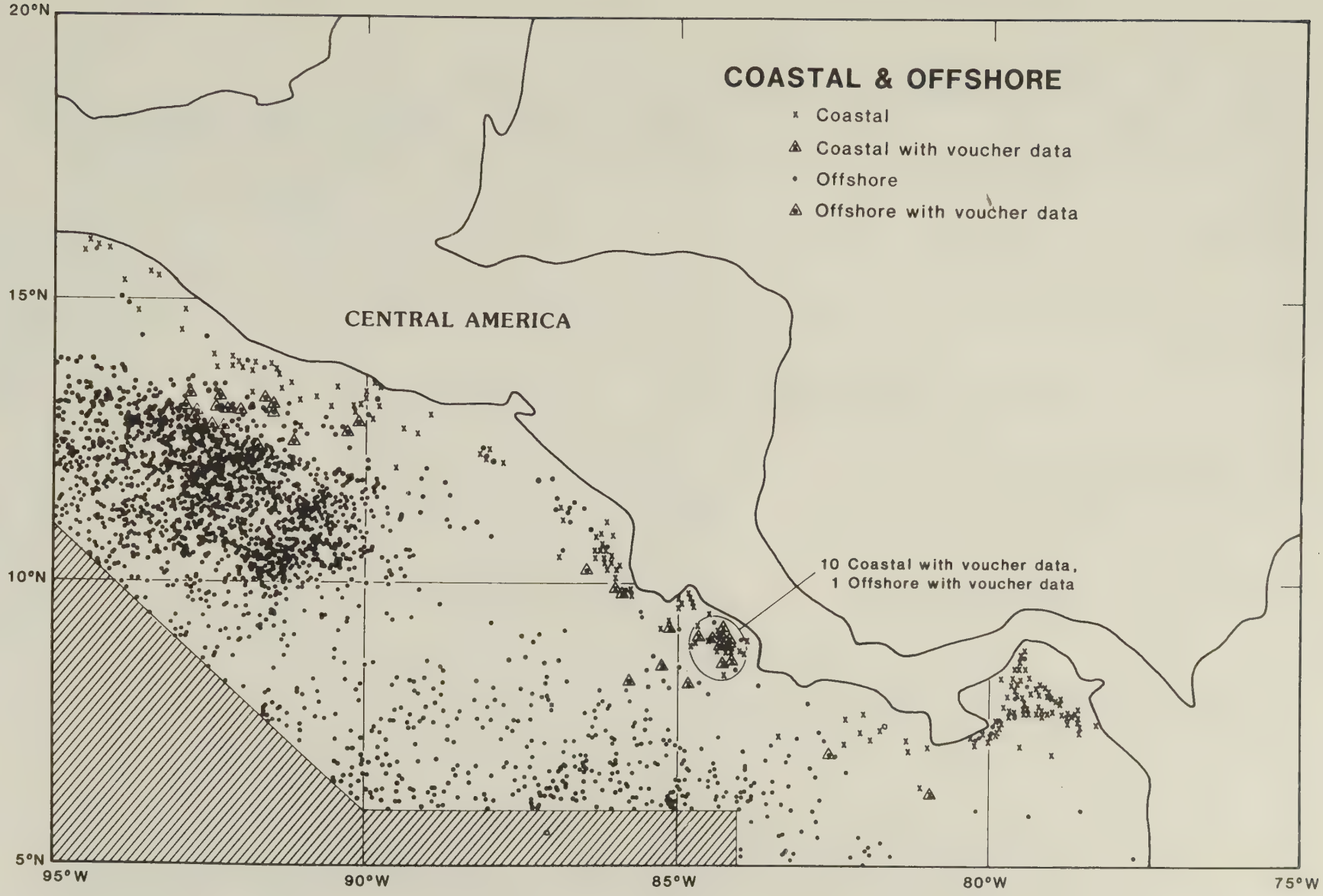
COASTAL & OFFSHORE
Coastal
Coastal with voucher data
Offshore
Offshore with voucher data
CENTRAL AMERICA
10 Coastal with voucher data,
1 Offshore with voucher data
20°N
15°N
10°N
5°N
95°W
90°W
85°W
80°W
75°W

Figure 10.

B

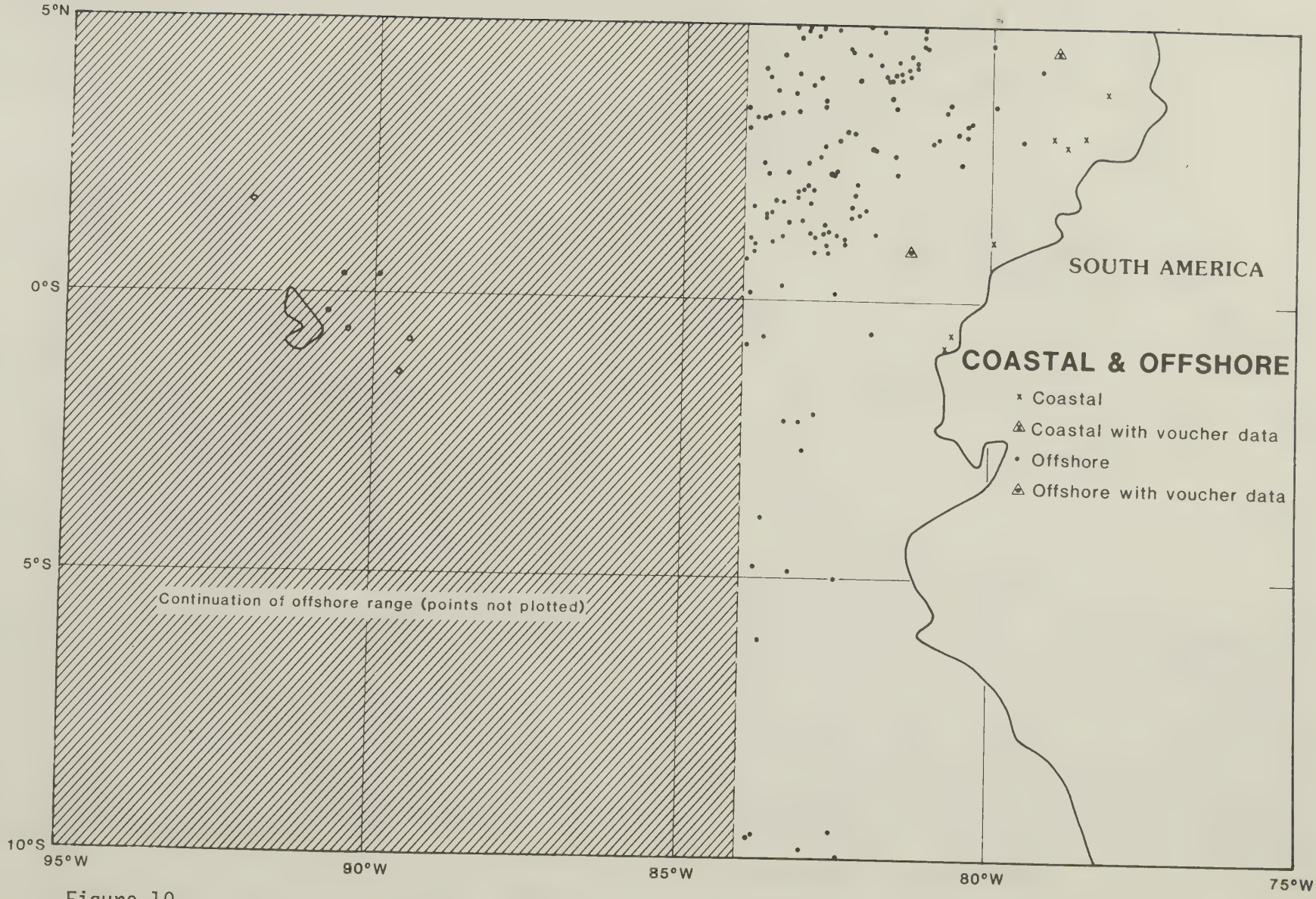
5°N
0°S
5°S
10°S
95°W
90°W
85°W
80°W
75°W
SOUTH AMERICA
COASTAL & OFFSHORE
Coastal
Coastal with voucher data
Offshore
Offshore with voucher data
Continuation of offshore range (points not plotted)

Figure 10.

C

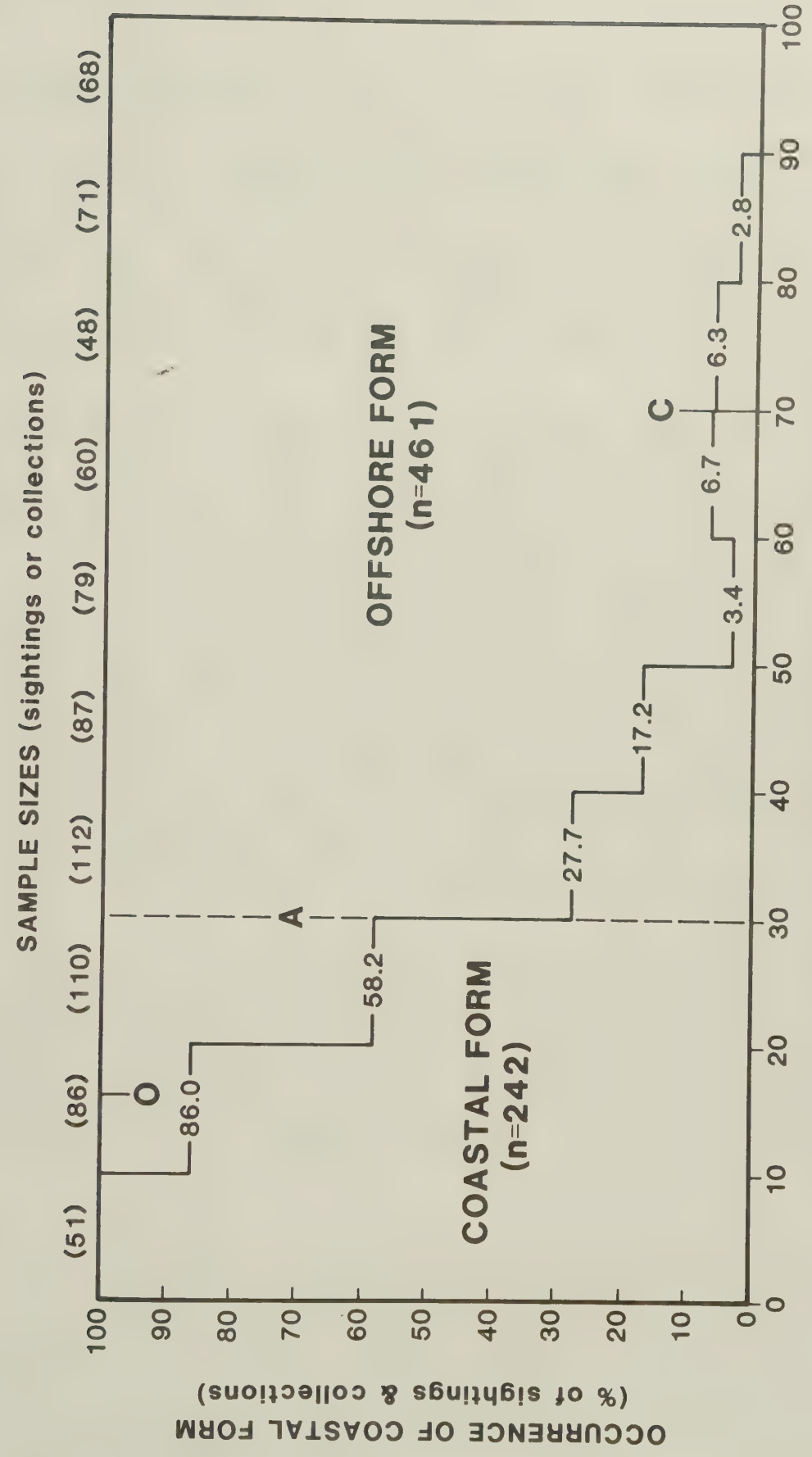

Figure 11. Relative abundance of records of offshore and coastal spotted dolphins by distance from coast. "C" is most offshore coastal record supported by photos, measurements or osteological specimens; "O" is most inshore offshore record with such support. "A" is distance from coast at which the proportion of included records that are offshore equals the proportion of coastal records that are excluded.

reverse. Another possible explanation is that coastal females continue to grow longer after attainment of sexual maturity than do offshore females.

The coastal form has been characterized as occurring in relatively "small groups or schools of fewer than 100 individuals" (Perrin 1975a, p. 127). In our review of sighting records, we found that while most records were of small groups of animals, there were also several records of very large schools of the coastal form (Table 2). Estimated school sizes ranged to 20,000 animals. Most of the very large schools were seen off Costa Rica, south of Puntarenas (~8-10°N and 83-85°W), while some were seen off central Mexico (~15°N latitude).

Schnell et al. (1982) concluded that the results of their multivariate analyses of skull data "fully warrant(s) the recognition of the southern S. attenuata as a distinct stock." They found the skulls of spotted dolphins from south of the equator to be on the average larger and to have a smaller temporal fossa than those of animals from north of the equator. They reached the same conclusion from analysis of body-length data; they found the southern animals to be on the average shorter than the northern animals. The results of our review of body-length data are the same (Figure 12). Males from the eastern portion of the SOPS '79 "northern offshore" range were modally about 3.5 cm longer than those from the "southern offshore" range (this difference and others between the offshore samples are statistically significant at $P<0.001$); the difference for females is 2.5 cm. When the southern sample is compared to the portion of the northern sample from west of 120°W, the difference is smaller, 2.0 cm for males and 1.3 cm for females, a result consistent with the finding by Schnell et al. (1982) of affinities between southern skulls and a very small sample of skulls from the far-western part of the northern range. The samples used in our body-length comparison covered the geographic range of the species more completely than did the samples of skulls available to Schnell et al. (Figure 5).

Two additional lines of evidence suggest that the southern animals are smaller than the northern animals: 1) Hohn and Hammond (1983) estimated length at birth from northern offshore samples at 85.4 cm. Their estimate from southern offshore samples was 83.2 cm. Their conclusion that the southern form is about 2 cm shorter than the northern form at birth is tentative because of the rather small sample size for the southern form. 2) Average length at attainment of sexual maturity was estimated at 177-180 cm (1974-1982) and 175 cm (1973-82) for northern and southern samples, respectively (Barlow, MS).

Because both females and males can continue to grow after attaining sexual maturity (Perrin et al., 1976), we considered the possibility that the differences between the northern and southern samples in average lengths of adults reflect not inherent racial difference in size but difference in age structure in the two regions. Samples from the southern region have not been aged, so direct comparison of age structures was not possible. We were able, however, to compare the frequency distributions of ovarian-corpus count for the two samples (Fig. 13). If ovulation rates are assumed to be similar in the two regions, it is clear that the age structures for adult females are not radically different. In any case, the difference is in a direction the

Table 2. Estimated school sizes for sightings of coastal and offshore spotted dolphins within 100 nm of the coast. Ranges of school sizes in parentheses.

School Size (no. of dolphins)	Coastal (n)	Form (%)	Offshore (n)	Form (%)
<100	144 (min. <10)	63.2	59 (min. <10)	13.2
100 - 1000	64	28.1	270	60.3
>1000	20 (max. >20,000)	8.8	119 (max. >20,000)	26.6
Total	228		448	

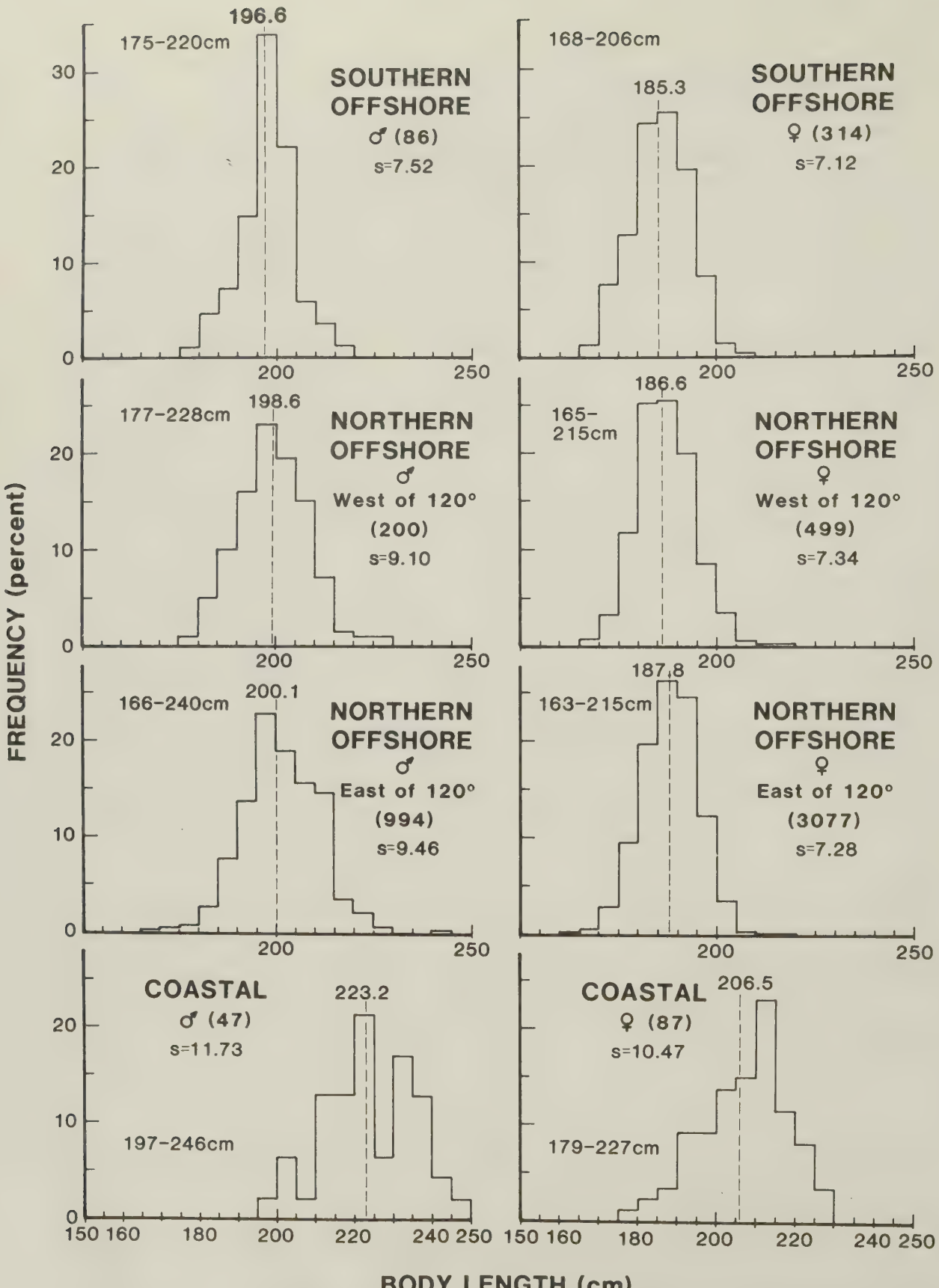

Figure 12. Frequency distributions ranges, means and standard deviations male and female spotted dolphins, S. attenuata, from four geographical areas. Sample sizes in parentheses.

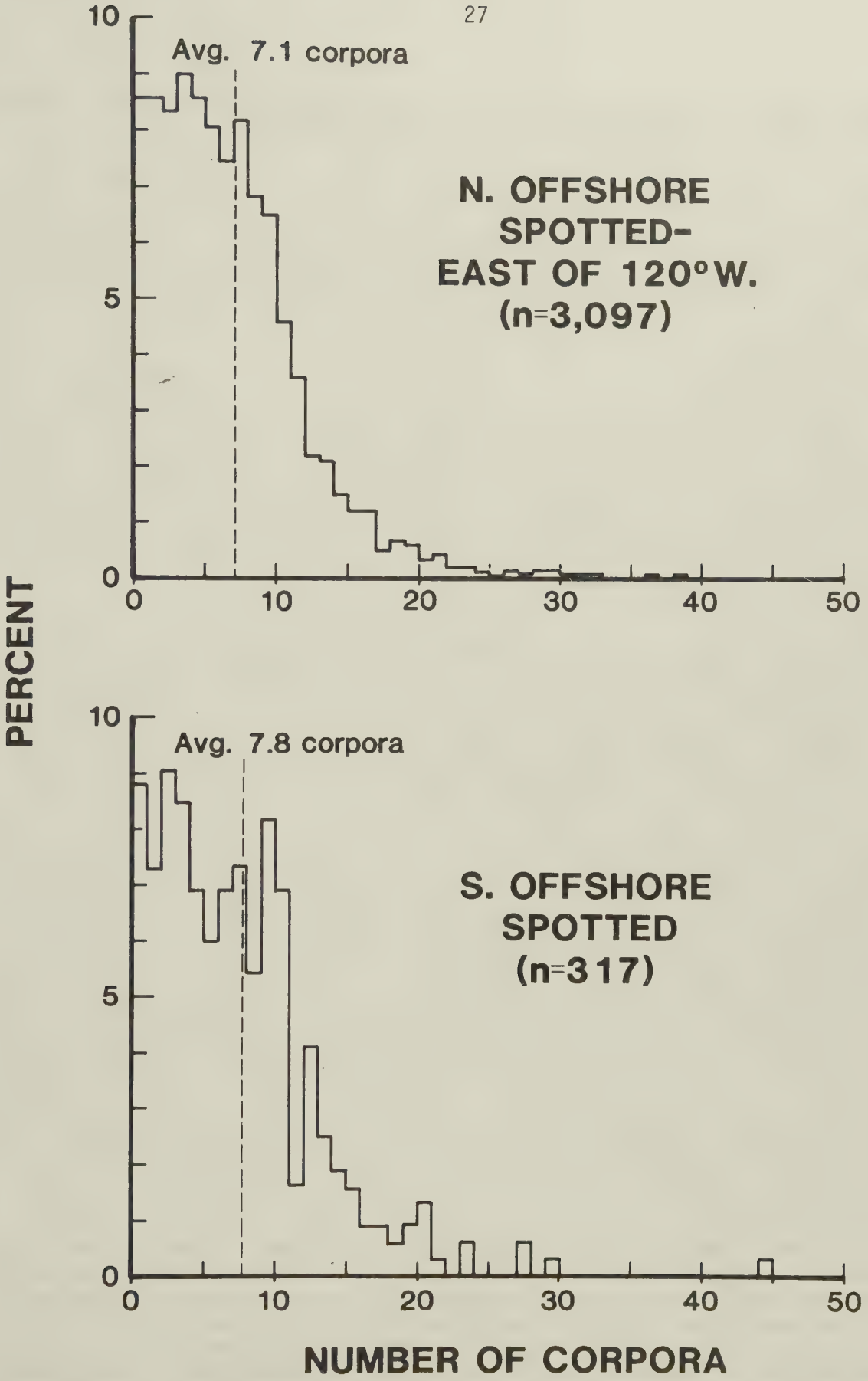

Figure 13. Frequency distributions of ovarian-corpus count for nothern and southern offshore samples of adult female spotted dolphins.

opposite of the direction that would be expected were the adult southern animals smaller because of being on the average younger.

The results of tagging studies (Perrin, Holts and Evans 1979; Jennings and Stives, 1979 and unpublished data) indicate considerable east-west movement within the northern offshore range. Of 206 tag recoveries or resights of tags or fin notches, 9 indicated movement from east to west of the 120th meridian; three involved movement of at least 1300 nm, over a period of 9-10 months. While this inference of long east-west movement must remain provisional (none of the 3 cases involved the actual recovery of a tag), when it is considered in the context of the east-west cline in morphology (body length, coloration and skull measurements), it suggests that such morphological differentiation is maintained despite at least temporary long-range movements of individuals and perhaps schools. One tag released north of 10°N was resighted by a tuna-seiner crewman (but not recovered) at 10° 37'S, some 4-5 months later. This result, if confirmed, would suggest that the apparent north-south morphological differences may actually reflect a clinal situation similar to that (east-west) which exists in the northern offshore portion of the range, rather than a substantial separation of populations north and south of the equator.

The results of a study of breeding seasonality (Barlow in press) show very different distributions of birth dates in southern than in northern offshore spotted dolphins (SOPS '79 boundaries). In the south the single calving season is quite short, March to May, whereas in the north there are two diffuse breeding peaks, in the spring and in the autumn. Barlow stratified the northern sample into two subsamples, from 0-5°N and from north of 5°N, and found an intermediate pattern in the equatorial stratum of a single but diffuse calving peak from March to June, statistically different from the patterns both to the south and the north. He concluded that these results support the view of a separate population south of the equator but that the transition from a diffuse bimodal breeding pattern in the north to a single sharp peak in the south may not be abrupt. He offered two possible explanations for the apparent patterns: 1) if seasonality in reproduction is determined by the timing of oceanographic or trophic factors, the difference could reflect geographical change in the timing of the environmental determinants, or 2) the area between 0° and 5°N could represent an area where two populations can occur, with the apparent distribution of birthdates actually being a composite of two different distributions. He noted that if a previously noted relative hiatus in sightings in the vicinity of the equator (Perrin, Sloan and Henderson 1979) is real, the latter explanation would be the least likely. The band of low density of sightings for 2-3° south of the equator is still present (Perrin et al. 1983) but not as well-defined as previously.

Hohn and Hammond (1983) have confirmed Barlow's results with modal-progression analysis of monthly distributions of length (after adjusting for use of different growth curves in the two studies), finding birth of two annual seasonal cohorts in the north but only one in the south. They also found a pattern of variation within the northern range, data from the far west and from along the equator not fitting well with the pattern in data from the more easterly and northerly major part of the range. They concluded that

while spotted dolphins may have different calving seasons depending on area of capture, this seasonality is probably "not actually a function of area but of schools or groups of schools which tend to inhabit different areas with different environmental conditions."

Resolution of the nature of the east-west and north-south variation must await study of more material from west of 120°W and from near the equator (see also the discussion below on origins of the geographical forms).

S. longirostris

In our review of records within 50 nm of the coast, we found only 33 convincing Costa Rican records, all south of the Gulf of Tehuantepec (Figure 14) and north of the Bay of Panama. Of these, 16 were supported by photos, measurements or specimens (Figure 15 and Table 3). We found no coastal records of eastern spinner dolphins with such support below the Gulf of Tehuantepec and only six unsupported records there. It appears that the eastern spinner dolphin is largely, or possibly totally, replaced on the coast below about 15°N by the larger, longer-beaked Costa Rican form. We ascribe the relatively small number of convincing records of either form to the difficulty of estimating size of animals at sea; the two forms are not known to differ in coloration. The sample of body lengths for the Costa Rican form taken directly from specimens is very small (Figure 16) but it is probable that modal adult length differs from that of the eastern form by about 30-40 cm in both sexes. A very large sample of photogrammetric lengths for both forms supports this conclusion (unpublished data, M. D. Scott).

We found several well supported records of the eastern form outside the SOPS '79 boundary (Figure 14); the range of this form extends farther to the west than previously documented, to at least 134°W, albeit in apparent very low density relative to that of the whitebelly form (Figure 17). We found only one well-supported record of the whitebelly form to the east of the SOPS '79 boundary (Figure 17). We attribute the large number of unsupported whitebelly sightings to the identification difficulties discussed in the Materials and Methods section and believe that many of them probably represent sightings of misidentified eastern spinners. In any case, the inshore density of whitebelly sightings is very low relative to that of the eastern form (Figure 14).

Rather than draw boundaries around what are believed to be the major ranges of the two forms as has been done in the past, we instead present a summary of relative frequency of records by 5-degree square (Figure 18; values in Appendix 5). The sample sizes on the fringe of the continuous range of the species in the ETP are small, but those in the major zone of overlap are very large, and the proportions likely reflect the true relative abundances of schools of the two forms. As discussed above, the real levels of whitebelly spinner dolphin records in the northeastern reaches of the eastern range are likely lower than indicated, e.g., we believe that the anomalously high proportion of whitebelly spinner dolphin sightings in the square at the tip of Baja California may be the result of unfamiliarity with the two kinds of spinner dolphins by south-bound first-time observers.

Table 3. Records of Costa Rican and eastern forms of S. longirostris within 50 nm of the coast (or a coastal island), north and south of Gulf of Tehuantepec (~15°N). Number of records supported by photos, body-length data or skull specimens in parentheses.

	Distance from coast (n. mi.)	Costa Rican form (records)	Eastern form (records)	Total
North of Gulf of Tehuantepec	0- 9	0	0	0
	10-19	0	8(1)	8(1)
	20-29	0	13(2)	13(2)
	30-39	0	7(0)	7(0)
	40-49	0	11(4)	11(4)
	Subtotal	0	39(7)	39(7)
South of Gulf of Tehuantepec	0- 9	3(2)	0	3(2)
	10-19	1(1)	1(0)	2(1)
	20-29	7(3)	5(0)	12(3)
	30-39	19*(9)	0	19*(9)
	40-49	3(1)	1(0)	4(1)
	Subtotal	33(16)	7(0)	40(16)
	Total	33(16)	46(7)	79(23)

*Includes 17 sightings made in a small area off southern Mexico during an aerial photogrammetric experiment by the Inter-American Tropical Tuna Commission in 1980 (see Figure 15). Other intervals contain records from this source as follows: 20-29 nm, 6; 40-49 nm, 1 (all Costa Rican).

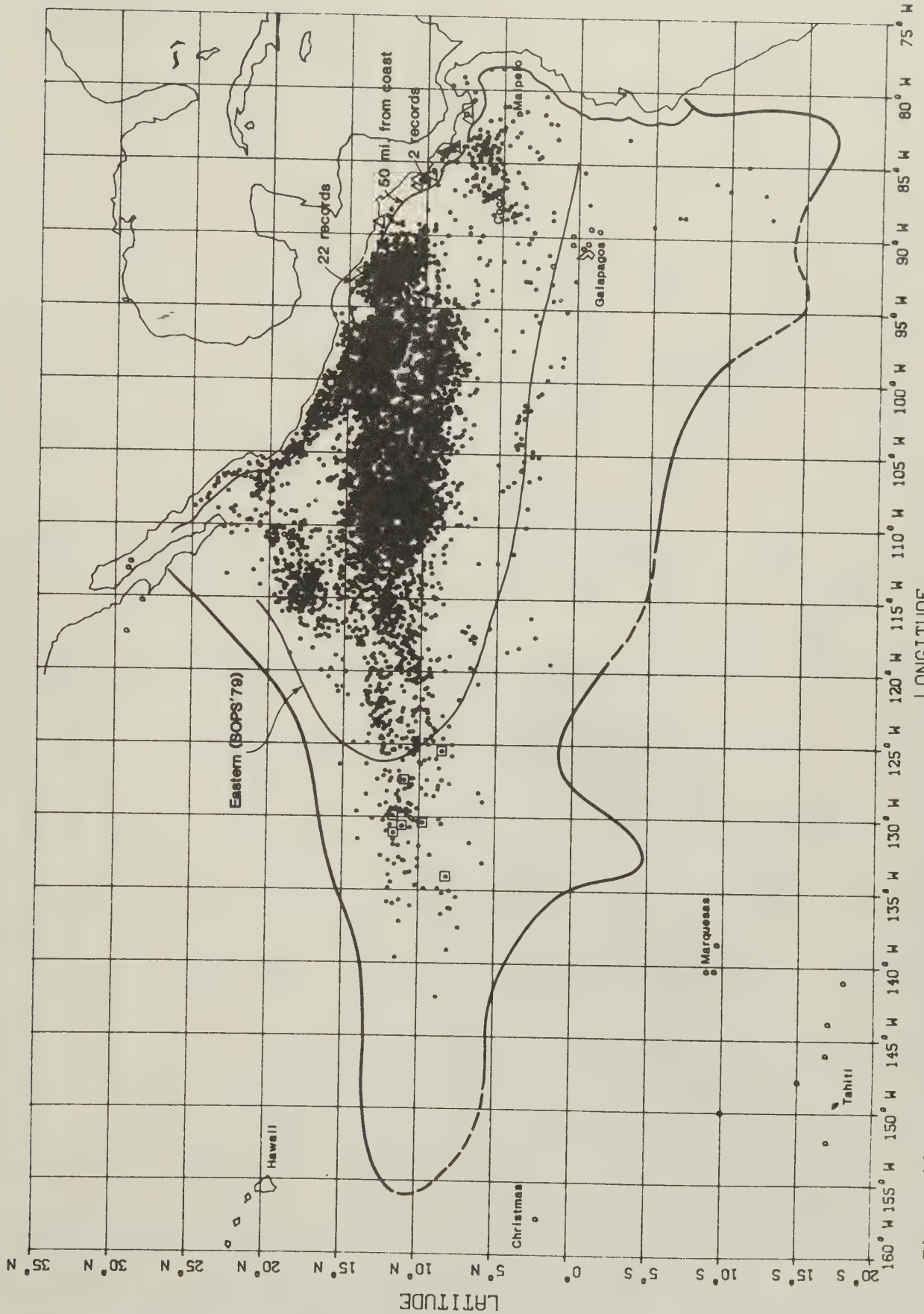

Figure 14. Distribution of eastern and Costa Rican spinner dolphins in the eastern tropical Pacific, showing records outlying the SOPS '79 boundary for the eastern form. Outlying records enclosed in squares are supported by specimen data.

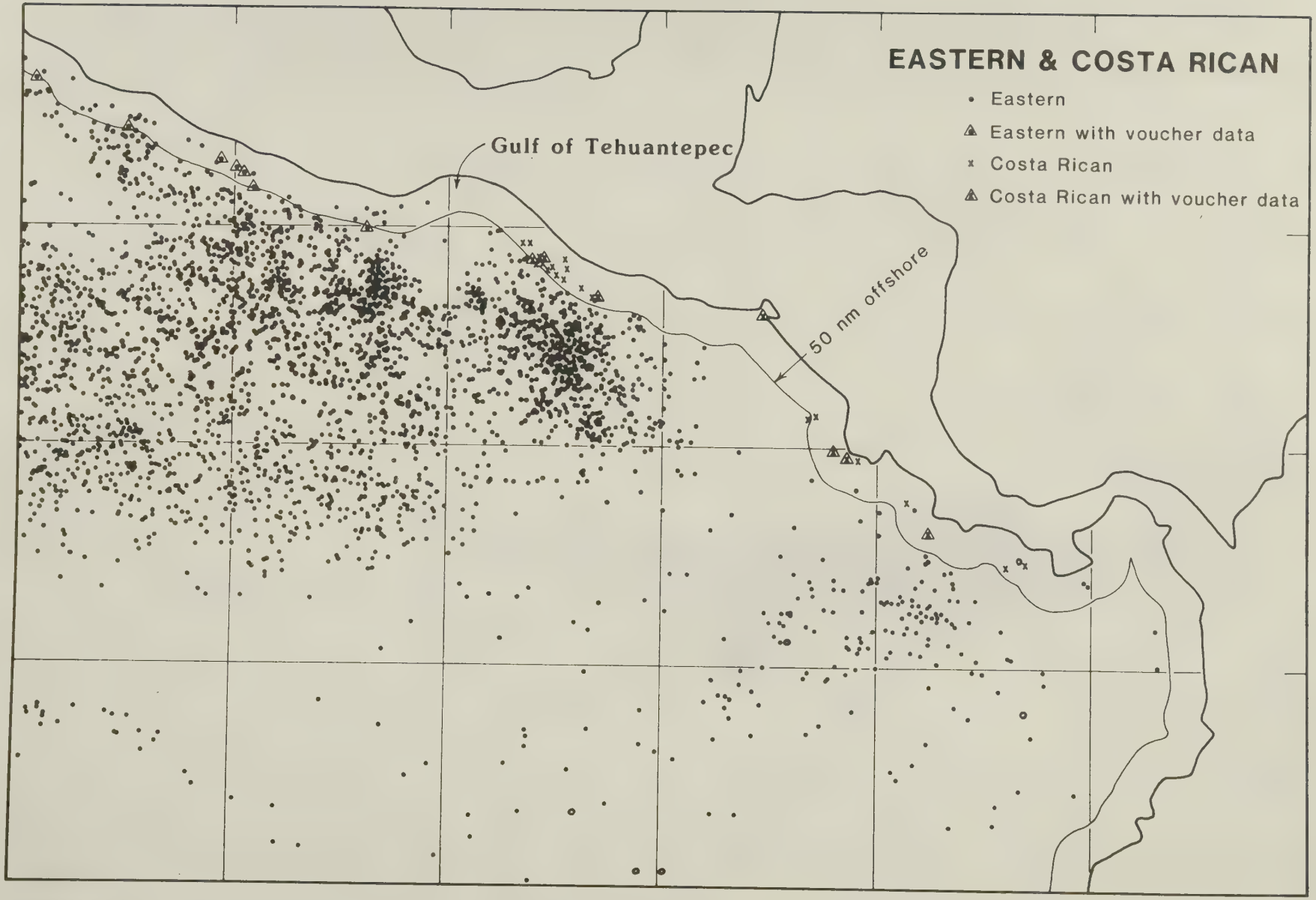

Figure 15. Distribution of eastern (dots) and Costa Rican (X's) spinners off Central America, with records inside 50 mi supported by photos, measurements or osteological specimens indicated (triangles for eastern and circled X's for Costa Rican).

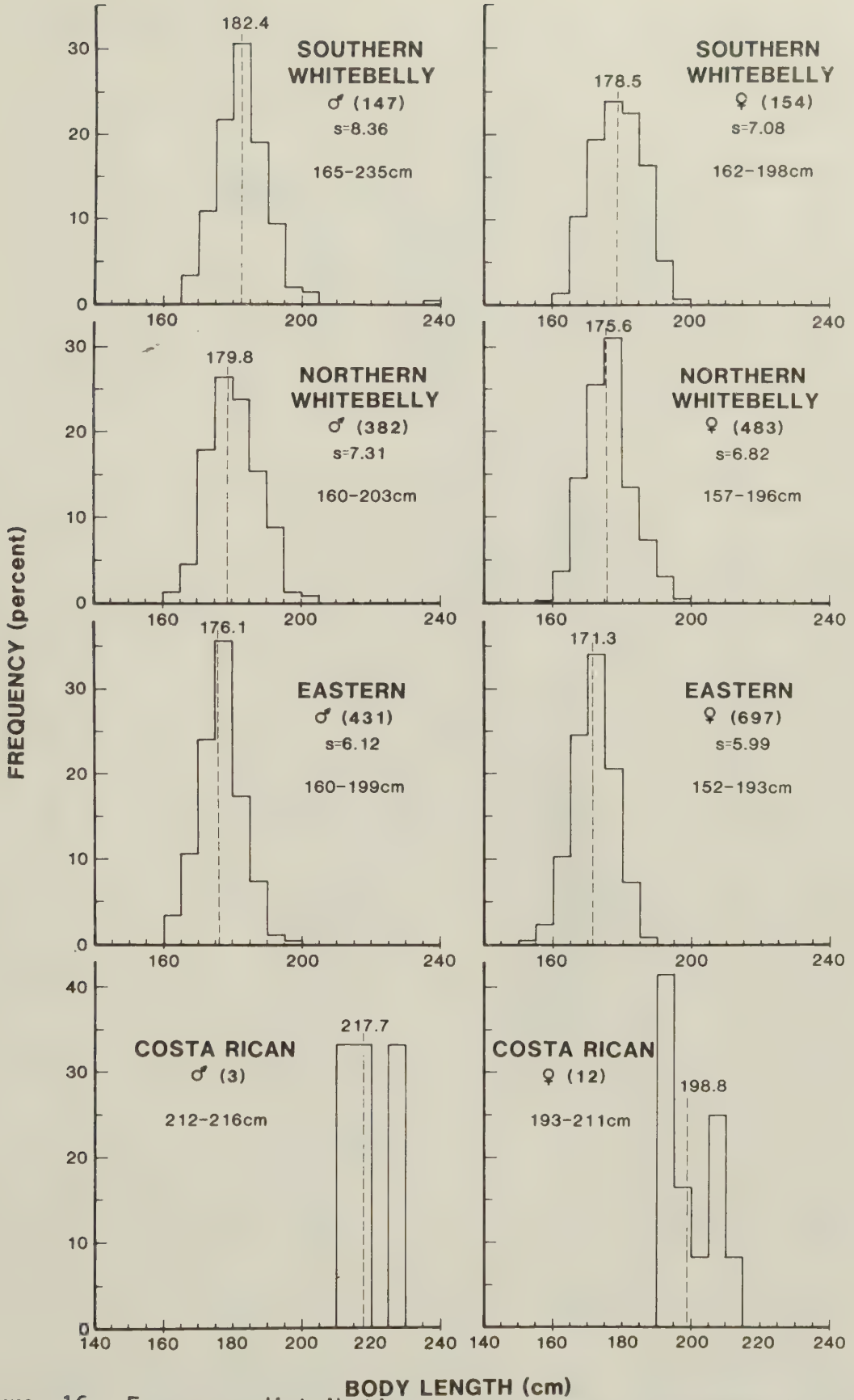

Figure 16. Frequency distributions, ranges, means and standard deviations of body length in samples of adult specimens of S. longirostris of four stocks. Sample sizes in parentheses.

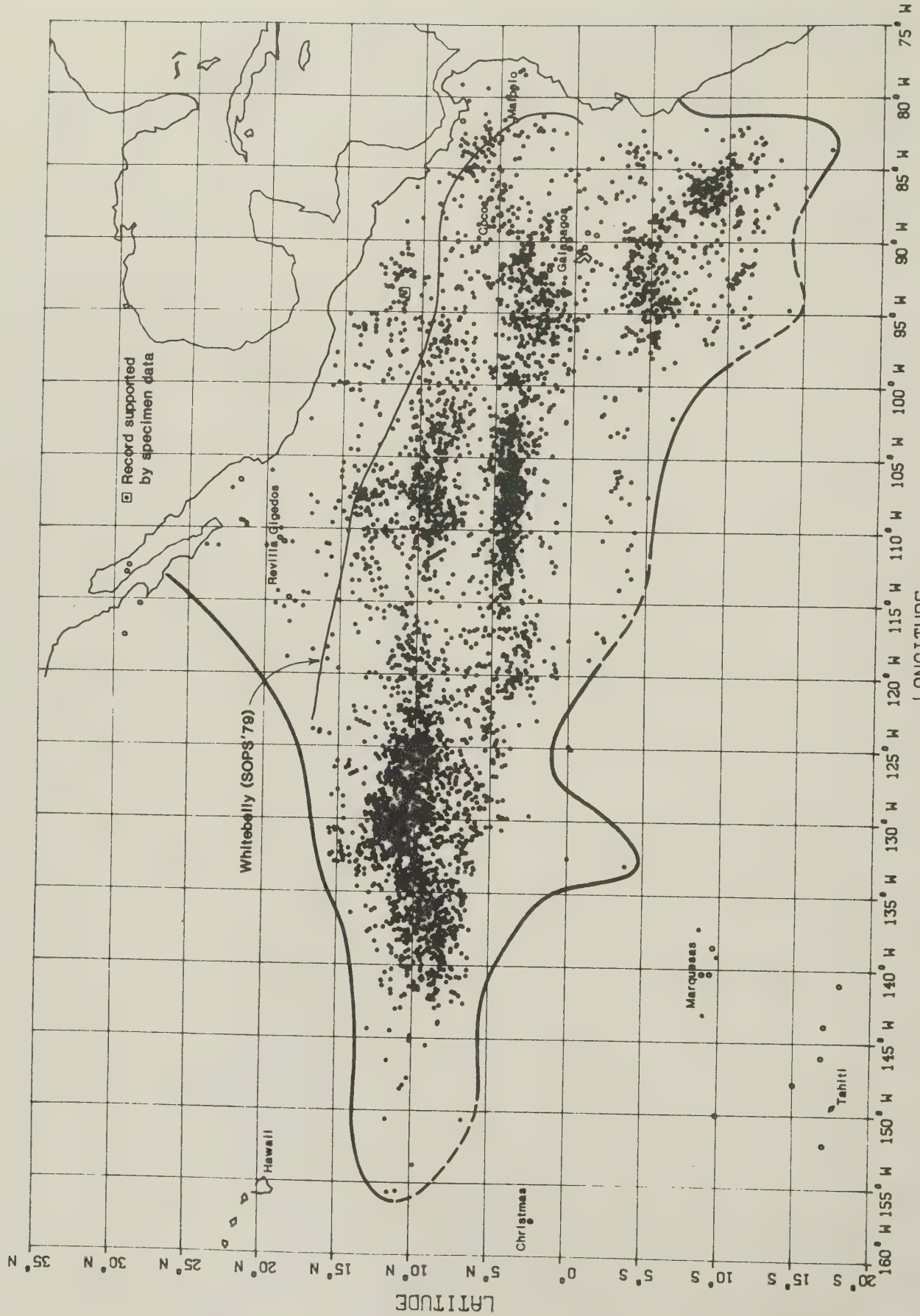

Figure 17. Distribution of whitebelly spinner dolphins (northern and southern) in the eastern Pacific, showing records east of the SOPS '79 boundary. Record enclosed in square is supported by specimen data.

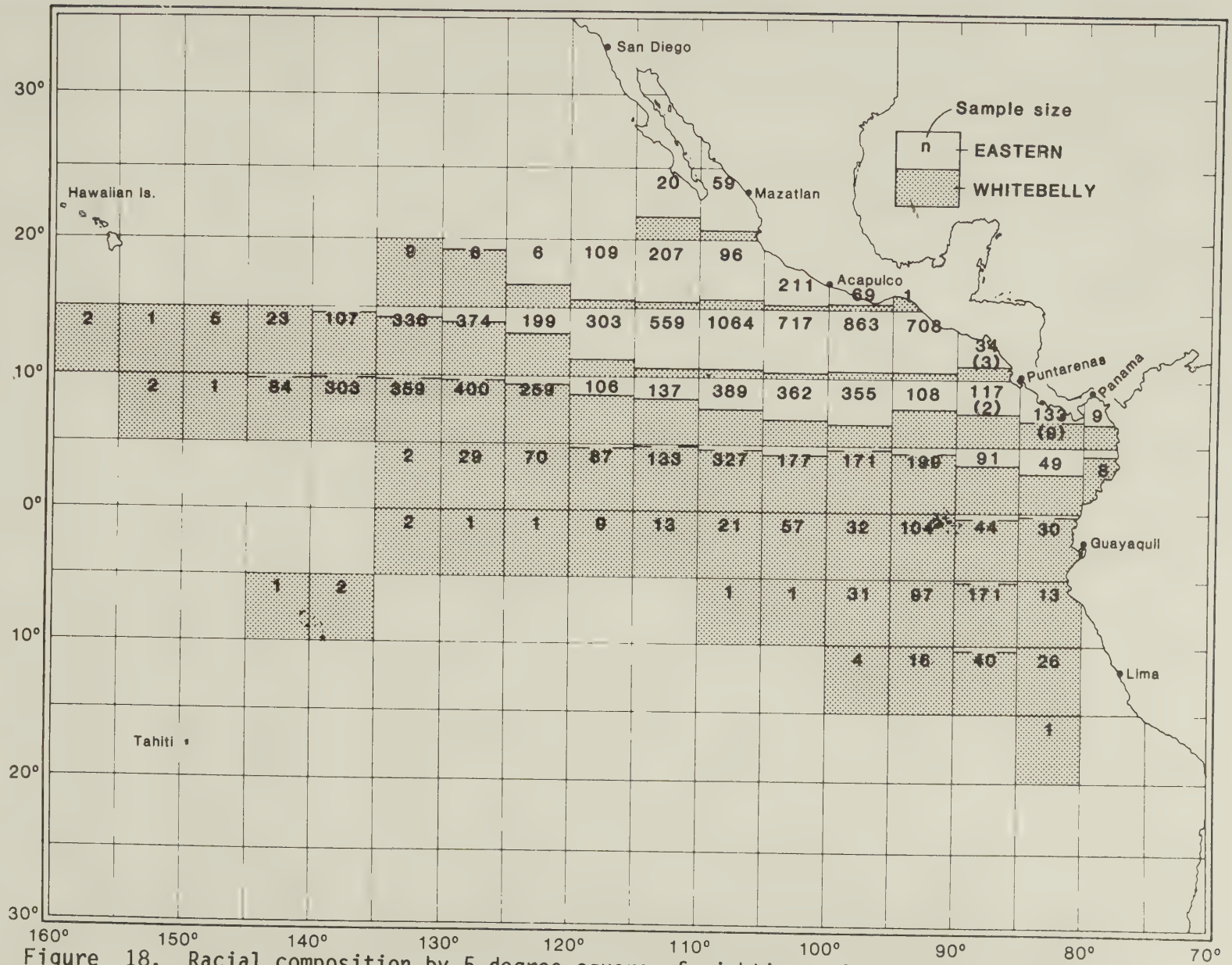

Figure 18. Racial composition by 5-degree square of sightings of S. longirostris identified to geographical race. Open areas of squares represent eastern form (and, for four squares, Costa Rican); shaded areas represent whitebelly form (northern and southern). Sample size given for each square. Number of Costa Rican records in parentheses.

Eastern spinner dolphin are on the average about 3-4 cm smaller (significant at $P<0.001$) than (northern) whitebelly spinner dolphins (Figure 16). The length-frequency distributions for the two forms are very similar in shape, and the variances are small compared to those for other samples examined here, suggesting that the two populations are well delineated and accurately represented by the samples.

Schnell et al. (1982) found "marked differentiation of a southern form from populations to the north" based on multivariate analysis of skull measurements. They found skulls from the south to be larger, with a proportionately larger temporal fossa, than skulls from the north, a situation exactly the opposite of that found in S. attenuata (smaller skulls, with larger fossae, in the south). As was the case for S. attenuata, they noted morphological affinities, in some of the analyses, between southern specimens and those from west of 120°W. They also found southern spinners to be longer than northern specimens. However, they did not distinguish between the eastern and whitebelly color forms. Our comparison of body length for northern and southern whitebelly spinner dolphins using the SOPS'79 ranges showed a difference of about 2-3 cm (significant at $P<0.01$ in males and females) (Figure 15). No new information is available on color pattern of the southern spinner dolphins beyond that given in Perrin, Sloan and Henderson (1979).

Because of the possibility that the difference in average body lenth could be caused by a difference in age structure (i.e., relatively more younger and smaller adult females in the northern region), we examined the frequency distributions of ovarian-corpus count for the two samples (Fig. 19), again assuming similar ovulation rates. The distributions do indeed differ, with a higher proportion having less than three corpora in the northern sample than in the southern sample. This may reflect differing age structures or differing ovulation rates; resolution of the question will require comparison of aged samples (not yet available for the southern form).

Tag returns for S. longirostris from the ETP have been few and suggest less extensive movement than do those for S. attenuata (Perrin, Holts and Evans 1979). There has been one sighting (by a yachtsman) of a tagged animal in the Marquesas (a spaghetti tag of unspecified type; unpublished data), where nine spinner dolphins were tagged in 1976 (Table 1). There have been no tag returns indicating movement across the equator or between the far-eastern and far-western parts of the ETP above the equator.

Barlow (in press) found a single sharp seasonal breeding peak in the eastern spinner dolphin and at least two modes in the northern whitebelly spinner dolphin. He also found a regional difference in timing of the peak in the eastern spinner dolphin, with offshore animals calving earlier in the year than inshore animals. He noted that distributional studies indicated that there are inshore and offshore population centers for eastern spinner dolphins with a decreased density of sightings in between (Figure 14 and Au et al. 1979) and suggested that a further subdivision of the eastern spinner into two populations/stocks would be meaningful. He did not examine seasonality in spinner dolphins south of the equator.

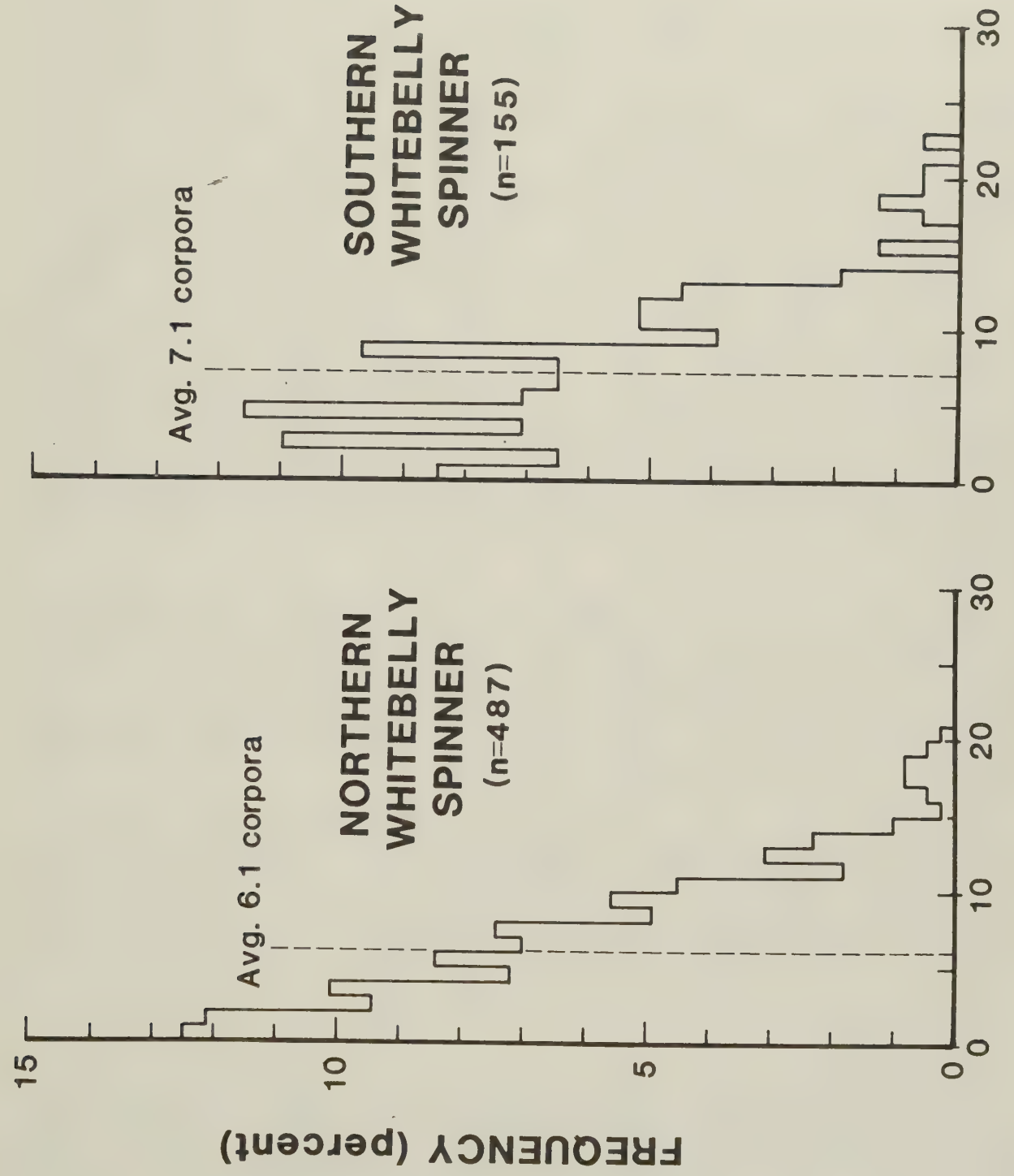

Figure 19. Frequency distributions of ovarian-corpus counts in northern and southern samples of adult female spotted dolphins.

S. coeruleoalba

Very little new information is available for this species. Delineation of the three tropical stocks was based on apparent latitudinal gaps in distribution, pending availability of adequate series of morphometric data (Au et al. 1979; Smith 1979, 1983). The band of relatively low density of sightings between 10 and 15°N is apparent in the data (Figure 20), but the distribution now appears relatively continuous south of 15°N and east of about 115°W, with a region of lower apparent density around the Galapagos Islands (which may only reflect the lesser sighting effort there -- Perrin et al. 1983, Figure 1). It would seem that there is now little or no justification for dividing the animals in this area (south of 15° and east of 115°W) into two stocks based on distribution data alone. The same applies to the eastern and western concentrations within the "central tropical" range; sighting effort has been relatively lower in the region between them. Only the low-density band between 10 and 15°N at this point can be said with some confidence to be real. There is a 200-300 nm-wide swath extending northeastward from 105°W where no striped dolphins have been sighted despite extremely high levels of sighting effort. We conclude that direct interchange between the population centers to the north and south probably occurs so seldom as to be negligible. In the region immediately to the west (between about 10° and 15°N and 105° to 120°W), where sighting effort has also been extremely heavy, there are only a few records of the species; the density here is apparently also very low.

In the area north of 25°N, where sighting effort has been extremely heavy to at least 31°N, scattered sightings of striped dolphins have continued to accumulate (Perrin et al. 1983) but it would appear that the animal occurs rarely in this warm-temperate part of its range in the eastern Pacific. It seems to us unlikely that this represents a separate population center. Similarly, the deduction of the existence of a "southern temperate" stock south of 10°S is probably also not justified.

The very limited adult body-length data (most of the animals killed have been juveniles) do not suggest a modal difference in length between animals from the northern and central tropical ranges (Figure 21). Only one adult (a 204-cm female) from the southern tropical range has been measured. Osteological specimens have been collected from all of the putative stocks but have not yet been prepared or studied (see Appendix 6).

Delphinus delphis

Although "Baja neritic" and "northern tropical" stocks were defined by Evans (1975, 1983) based on morphology and color patterns (Figure 4), these have been pooled in assessment and management (Smith 1979, 1983; Holt and Powers 1982). Common dolphins sampled in the fishery and tropical sightings have been identified only as "Delphinus delphis" and allocated by position to the "northern tropical" (between 15 and 28°N) "central tropical" (3-15°N) or "southern tropical" (3° N° - 10°S) latitudinal management units. This pooling is evident in the "northern tropical" body-length data (Figure 22); the Baja

Figure 20. Records of S. coeruleoalba in the eastern Pacific. Boundary from Perrin et al. 1983.

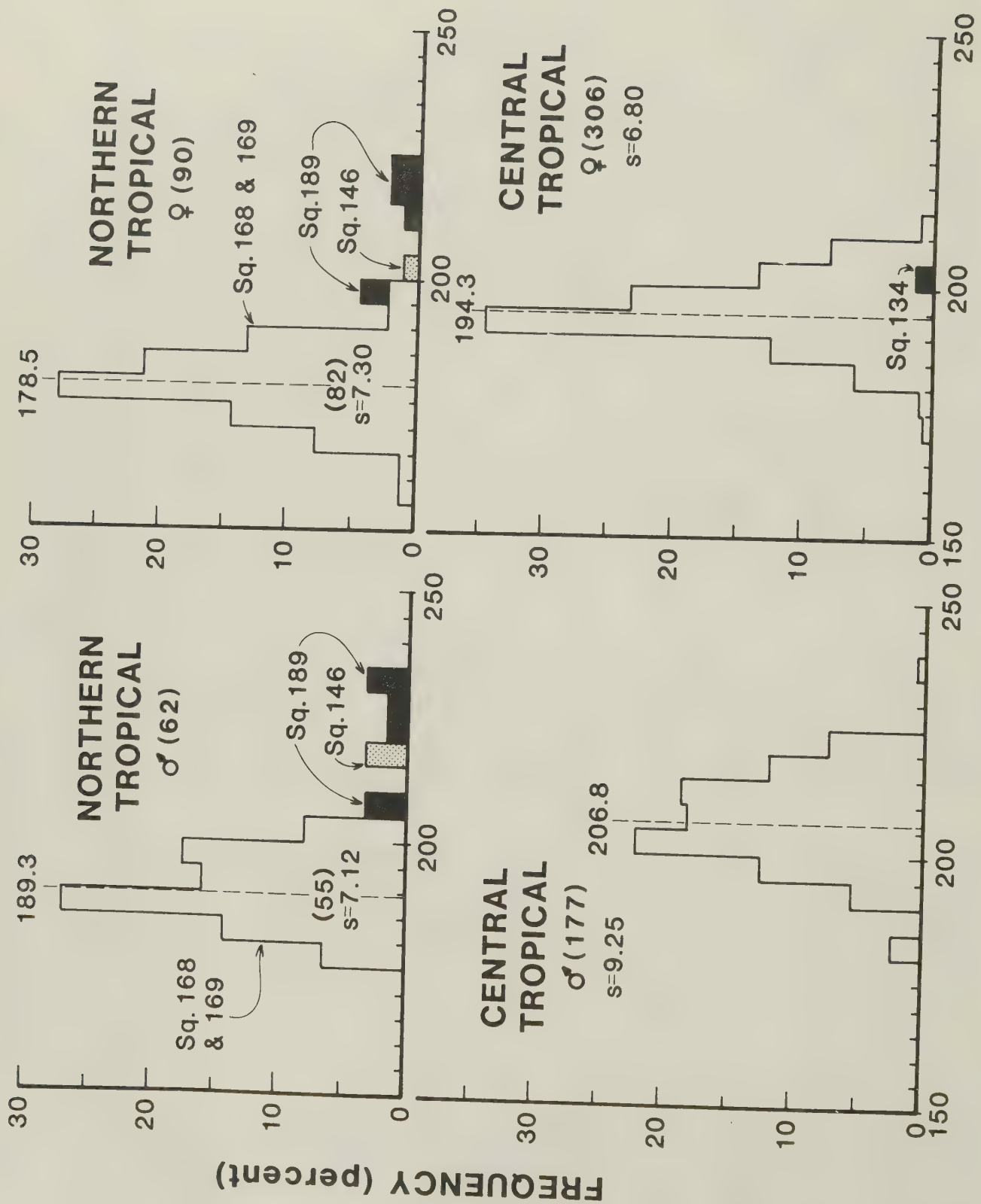

Figure 21. Length-frequency distribution and means for northern tropical and southern tropical adult males and females of S. coeruleoalba. Sample sizes in parentheses.

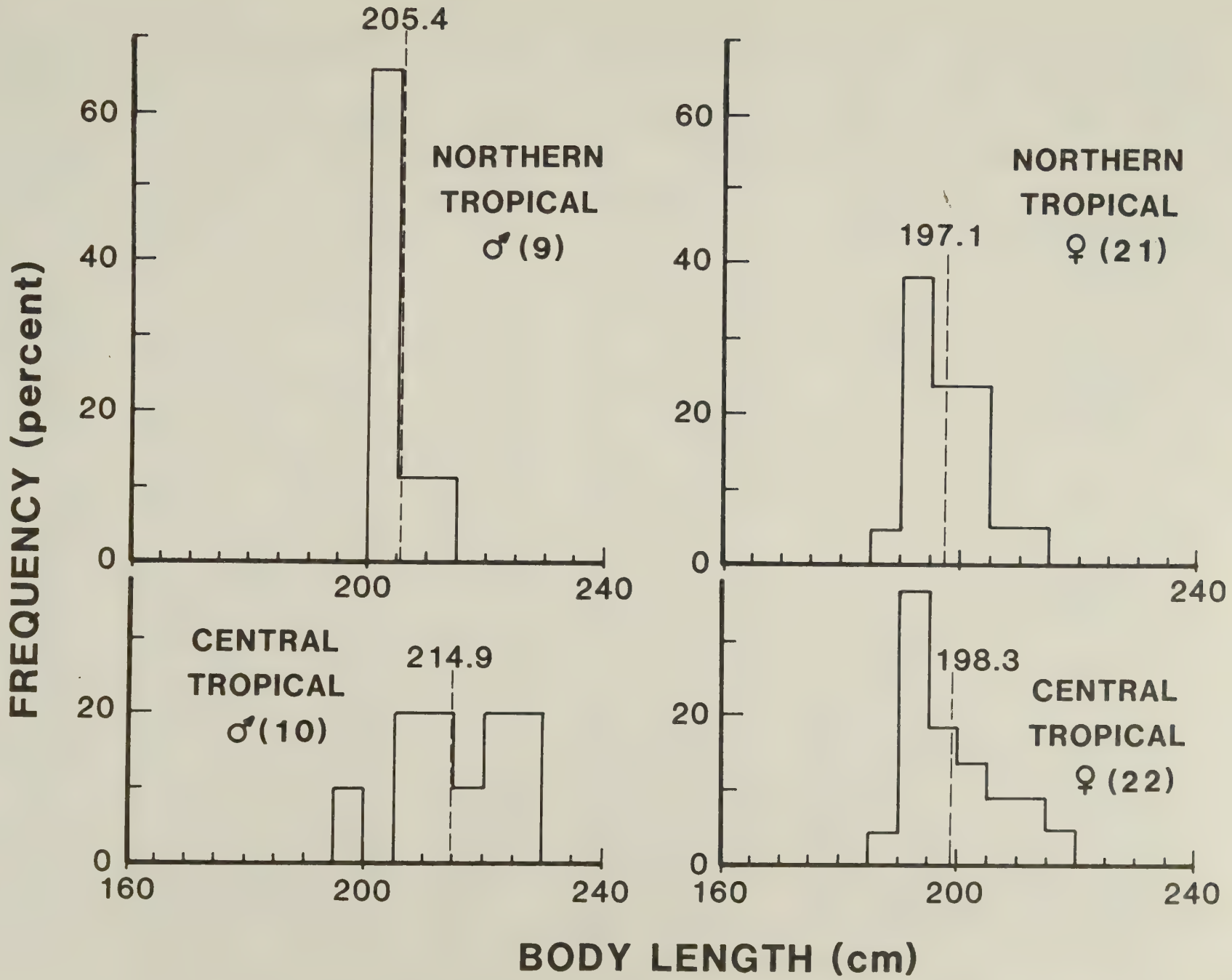

Figure 22. Frequency distributions, ranges, means and standard deviations of length in two stocks of Delphinus delphis. Sample sizes in parentheses.

neritic form is about 30 cm longer than the northern tropical form (Evans 1983). The animals included in the "northern tropical" sample came from two areas, Baja California (Squares 168, 169 and 189 in Figure 8) and off southern Mexico (Square 146). Those from north of Magdalena Bay (Square 189) appear from their lengths (shaded portions of histograms in Figure 20) to have been of the Baja neritic form, whereas those from south of Magdalena Bay and around Cabo San Lucas into the Gulf of California (Squares 168 and 169 in Figure 8) appear to have been of the short-beaked northern tropical form. Evans (1983) showed the range of the Baja Neritic form as including the Gulf of California. Some of the Baja Neritic common dolphins on the outer coast were taken more than 50 miles offshore, and some of the short-beaked "offshore" animals were captured within 10 nm of the coast (Table 4). When this is considered in the context of the pooled distribution data (Figure 23), it is clear that common dolphins off Baja California cannot be identified to stock on the basis of an inshore-offshore criterion alone. The two forms are however fairly easily identified at sea by size, shape and coloration (Leatherwood, Reeves, Perrin and Evans 1982).

In addition to the specimens indicated in Figs. 8 and 2, there were 21 animals from Square 189 measured for which gonadal material was not collected that would allow them to be classified as adult or immature. The lengths of 12 males were 153, 164, 195, 208, 218, 225(2), 227, 228, 230 and 236 cm. The lengths of 9 females were 181, 197(2), 199, 205, 206(2), 209, 213 and 215 cm. These lengths more likely belong to the same frequency distributions as the adult animals from square 189 than to those of the animals from squares 168 and 169 just to the south. Therefore, maximum length of the Baja Neritic form can be assumed to be at least 236 cm.

The sample from off the state of Guerrero in southern Mexico (Square 146) is too small (2 males and 3 females, cross-hatched in Figure 22) to allow a firm conclusion to be made, but it apparently does not belong to the same distribution as the animals from squares 168 and 169.

Evans initially (1975) did not subdivide the short-beaked "temperate - subtropical" animals north of 20°N into temperate and tropical stocks. In Evans 1976a and b (and repeated in Evans 1983), he defined a "northern" stock in the ETP extending from about 16-18°N to just below Cedros Island (about 28°N), but did not delineate a "temperate" stock to the north. The 1979 assessment used "northern temperate" and "northern tropical" management units divided at 28°N. The very extensive distribution data do not now suggest a gap or transition of any sort down the entire length of Baja California, and the "northern tropical" body-length data (Figure 22) accord precisely with Evans' (1975) pooled sample of all short-beaked "temperate-subtropical" animals from north of 20°N. Thus no evidence exists to support to dividing the short-beaked common dolphins at 28°N.

Evans (1975) found short-beaked common dolphins from south of 15°N ("central tropical") to be modally longer than those from north of 20°N as well as differing from them in skull features and possibly in color pattern. The present larger sample of central-tropical length data (177 males and 306 females, vs 40 males and 48 females in Evans (1975)) confirms this; the difference is approximately 18 cm in males and 16 cm in females. With the

Table 4. Distances from coast of specimen records of Delphinus delphis in square 189 (Baja Neritic form; north of 25°N) and squares 168-69 (northern tropical form; south of 25°N). Most offshore record of Baja Neritic at 51 nm; most inshore northern tropical at 51 nm. See Figure 8 for locations of squares and Figure 22 for specimen data.

Distance from coast (nm)	Records	
	Baja neritic /Sq. 189 (no.)	Northern tropical /Sq. 168 & 169 (no.)
0 - 9		1
10 - 19	1	7
20 - 29	2	7
30 - 39	2	10
40 - 49	4	12
50 - 59	1	12
60 - 69		8
70 - 79		9
80 - 89		4
90 - 99		6
Total	10	76

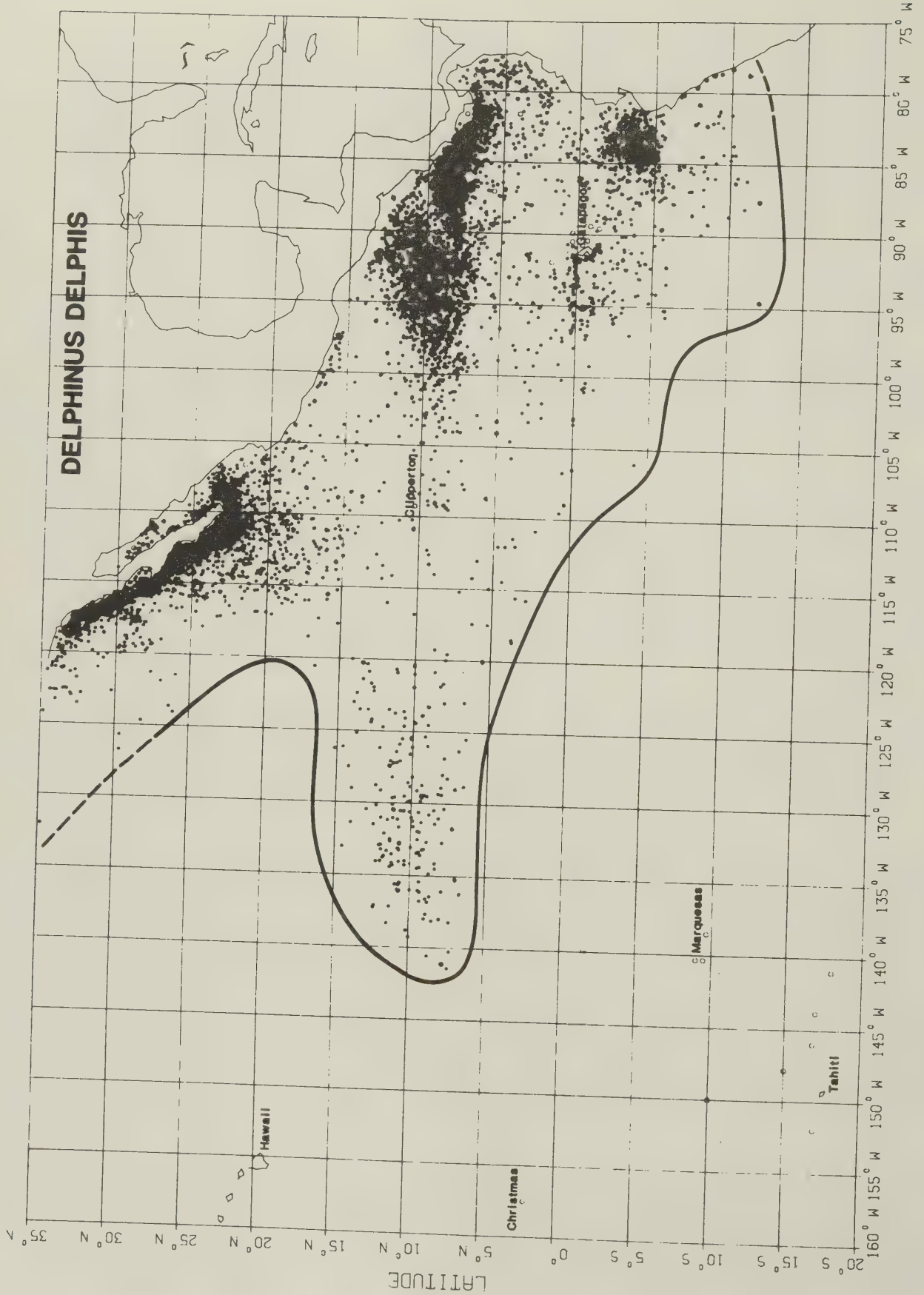

Figure 23. Records of Delphinus delphis in the eastern tropical Pacific. Boundary from Perrin et al. 1983.

exception of the local concentration of records off southern Mexico between about 97° and 103°W (Figure 23), the central-tropical concentration (centered around 8-10°N) is separated from the northern-tropical concentration by an 800-nm-deep zone in which sighting effort has been heavy and sightings of common dolphins rare (only a dozen or so, compared to several thousand sightings of other species). This separation and the morphological differences speak strongly for treating the two populations as separate stocks. The coastal animals from between 97° and 103°W are problematical; their lengths don't accord well with the distributions for either the "northern tropical" or the "central tropical" samples, although they fit best with the latter. Determination of their affinities with any confidence must await study of osteological material and accumulation of more length data. Provisionally, they could be included in the central-tropical unit. They may prove to comprise a separate population, however, and it would be equally reasonable to treat them separately at this time.

Length was available for only one (female) common dolphin from the far-western portion of the central-tropical range (square 134 in Figure 8); it is within the central-tropical range of length (shaded in Figure 22). The number of records of the species from west of 120°W is small (Figure 23), despite heavy sighting effort (Perrin et al. 1983) and the distances separating the area from the denser population centers to the east are large. Determination of affinities must await more information.

Evans (1975, 1983) did not examine material from south of 3°N, the "southern tropical" range. Length data are available for only 6 adults (females: 180, 182, 188, 189, 194, and 198 cm). These accord about equally well with the length distributions for the central tropical and the northern tropical samples (Figure 22). Since the distribution of the common dolphin in this area exhibits a largely reciprocal relationship with that of the spotted and spinner dolphins, being abundant in regions likely to have lower sea-surface temperatures (near the Galapagos Islands and near the coast of Peru at 0-5°S) than do the areas where those species are abundant (Perrin et al. 1983), it is possible that the concentration near and below the equator represents a temperate-tropical stock analagous to the short-beaked northern temperate-tropical stock. There is fairly good separation from the central-tropical center by a band of heavy sighting effort between 0° and 5°N.

ORIGINS OF THE GEOGRAPHICAL FORMS

The results for Stenella spp. suggest that a concept of radially patterned geographical variation in the ETP may be more appropriate than the primarily latitudinal approach that has held sway to date. The radial pattern also meshes better with our developing understanding of the ecology of pelagic dolphins in the ETP. Perrin (in press) has suggested that the variation between central Pacific and eastern Pacific races of Stenella attenuata and S. longirostris may actually constitute ecological character displacement between the two species in the ETP, where they school and feed together. (They school and feed separately elsewhere). Under this hypothesis, the animals forage

together because of mutual advantage gained in finding prey or in avoiding predators* in the special conditions of the oceanographically anomalous eastern tropical Pacific**, and their divergence in coloration, tooth size, jaw muscles etc. reflects divergent specializations in feeding (species, size and depth of prey) that minimize direct competition between the components of the multi-species "school" (which also often includes yellowfin tuna). The two species (and the tuna) do indeed have different feeding habits in the ETP, even in the same "school" (Perrin, Warner, Fiscus and Holts, 1973). In addition, Schnell et al. (1982) found that expression of characters of the skull in S. attenuata that are associated with feeding is correlated with environmental parameters over long distances in the ETP. For example, a correlation exists between size of the temporal fossa (through which the main jaw-closing muscle passes) and sea-surface temperature, solar insulation and thickness of the oxygen-minimum layer. S. longirostris varies in a similar way. Schnell et al. (1982) concluded that "the rather marked morphological covariation between S. attenuata and S. longirostris involving a number of characters could reflect common causes associated with environmental spatial variation."

A conceptual model of the radial nature of the pattern of variation can be based on what we now know in a general way (Fig. 24). In this view, the animals in the far eastern Pacific (the eastern or Costa Rican spinner dolphins and, for the sake of arguement, the offshore spotted dolphins north of the equator and east of 120°W), and the dolphins in the central Pacific (Polynesia and points west) comprise the purest populations of the ecologically differentiated forms. Those in between (whitebelly spinner and offshore spotted dolphins south of the equator and west of 120°W) would thus comprise "hybrid" swarms. At least two historical scenarios can be suggested: differentiation during isolation of populations in the far-eastern Pacific by cool-water communication between the hemispheres during a glacial epoch (as has been suggested for the tropical Atlantic -- Perrin, Mitchell and van Bree 1978), or existence, now or in the past, of selection pressures in the far-eastern Pacific sufficiently strong to give rise to differentiation without isolation by a physical barrier. In either case, the present situation of pronounced polymorphism could be stable or could be dynamic, e.g., introgression of central Pacific genes from the west could be neutralized by continuing strong selection pressures in the ecologically different eastern Pacific, or the Indo-Pacific pool could be in the process of swamping out the eastern-Pacific differentiation. Lacking historical data, this of course is only speculation. Analysis of existing osteological material from Polynesia

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*Norris and Dohl (1980a) have suggested that ETP spinner dolphins may use the shelter of spotted dolphin schools as a surrogate for the shallow bays in which they spend their daytime resting hours in the central Pacific.

**The eastern Pacific is peculiar in having a relatively thin, warm mixed layer (~50 m thick) above a stable steep thermocline and a thick oxygen minimum layer. This establishes an effective shallow habitat much like the nearshore habitat in other tropical waters (see Perrin, Coe and Zweifel 1976 and Au et al. 1979).

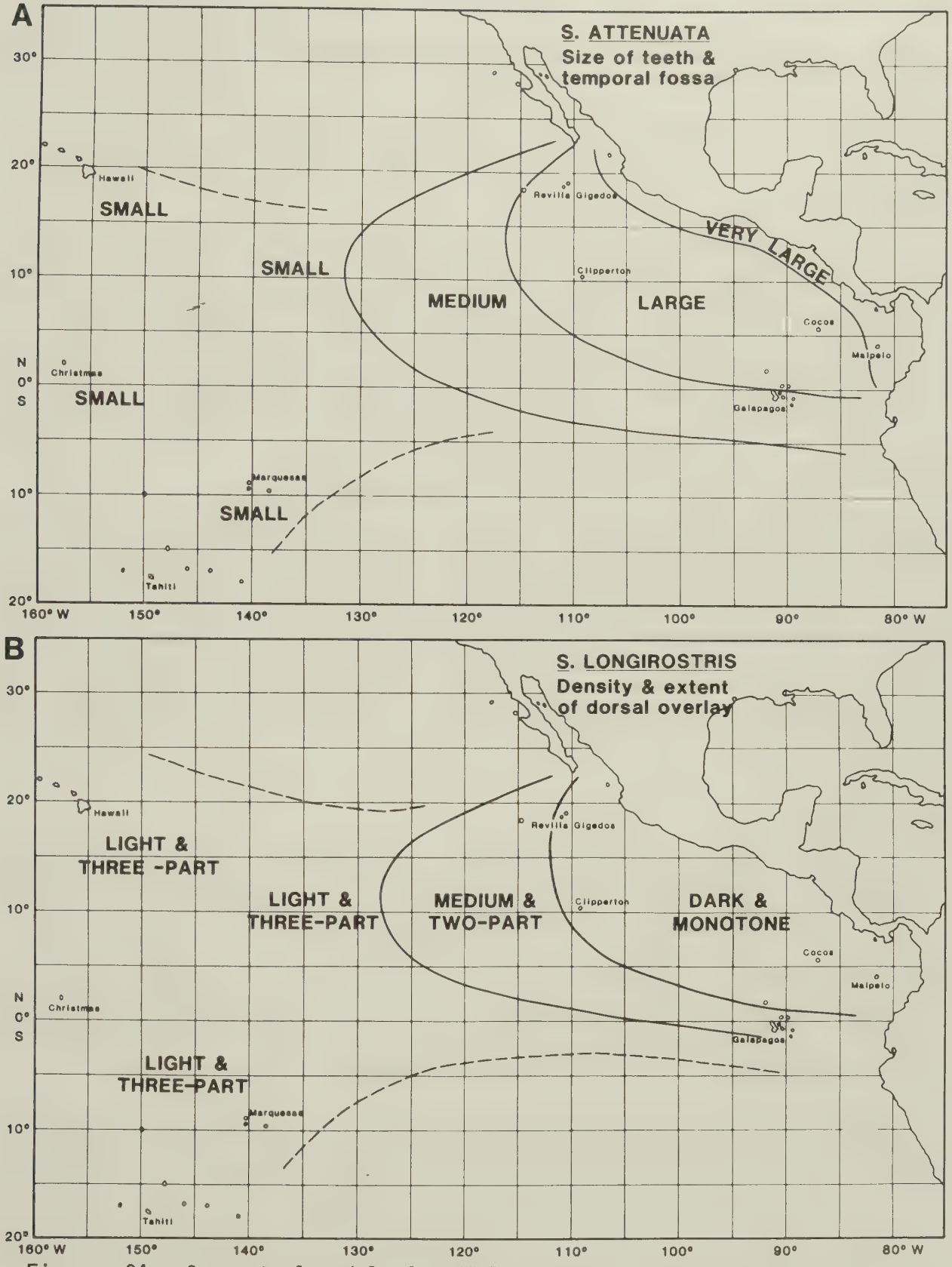

Figure 24. Conceptual model of radial pattern of geographical variation in pelagic populations of Stenella A) S. attenuata and B) S. longirostris in the eastern tropical Pacific. Color pattern information from Perrin 1972a and Perrin et al. 1979.

(mainly Hawaii) may shed some light on relationships between animals there and those in the outer reaches of the ETP.

RECOMMENDATIONS

S. attenuata

1. Schools should not be identified as coastal or offshore on the basis of position alone, because the ranges of the two forms overlap. Any school within 100 nm of the coast for which size and degree of spotting of the animals is not determined should be relegated to unidentified status. If a management boundary is set inside 100 nm to balance errors of identification based exclusively on position, it should take into account relative school sizes for the two forms as well as relative abundance of schools, in order to know what proportion of the population would be protected at various distances from the coast.

2. The northern and southern samples are clearly morphologically distinct. Although the spotted dolphins west of 120°W show affinities with those south of the equator, and though the east-west and north-south variation may be broadly rather than sharply clinal, the present division of offshore populations into northern and southern units should be retained pending study of material from west of 120°W, from the equatorial region, and from Hawaii (see Appendix 6) and results of ongoing studies of mitrochondial DNA (see Appendix 5). Consideration should also be given to seasonal and year-to-year variation in oceanographic regimes north and south of the equator and in the area between the two apparent centers of distribution.

S. longirostris

1. South of 16°N latitude, north of 7°N and within 50 miles of the coast, schools of spinner dolphins should be assigned to Costa Rican or eastern based on modal body length and relative beak length. If this is not possible, they should be called unidentified spinner.

2. Identification of spinner schools as eastern (or Costa Rican) or (northern or southern) whitebelly should be based on modal adult color pattern and modal adult-male dorsal-fin shape. Assessment and management of the two forms in the overlapping portions of their range should be on an area-by-area basis (e.g., 5-degree squares, as in Figure 18).

3. As in the case of the spotted dolphin, the division of whitebelly spinners into northern and southern management units should be retained pending study of material from areas poorly represented in previous studies (near the equator and in the far west area) and comparison of the age structures of the northern and southern samples. Existing osteological material from Hawaii should be analyzed to determine relationships with animals in the ETP. Seasonal and year-to-year oceanographic variation should also be considered in future definition of units.

S. coeruleoalba

A single provisional division into northern and southern stocks is recommended (Figure 25). As this is based solely on a hiatus in distribution, the existing osteological material should be analyzed.

Delphinus delphis

1. Within 100 nm of the Pacific coast of Baja California and in the Gulf of California, schools of common dolphins should be identified as Baja neritic or northern (temperate/tropical) based on modal length, coloration and relative beak length. If these features are not observable, the school should be classified as unidentified common dolphin.

2. Division into northern, central and southern units is recommended (in addition to the Baja neritic stock, which is contained within the northern range) (Figure 26). As the central - southern division is based on distribution alone, material from the southern area should be collected and compared to existing material from the central area.

3. Delineation of a Guerrero unit of common dolphins off southern Mexico is marginally justified pending study of material from the area.

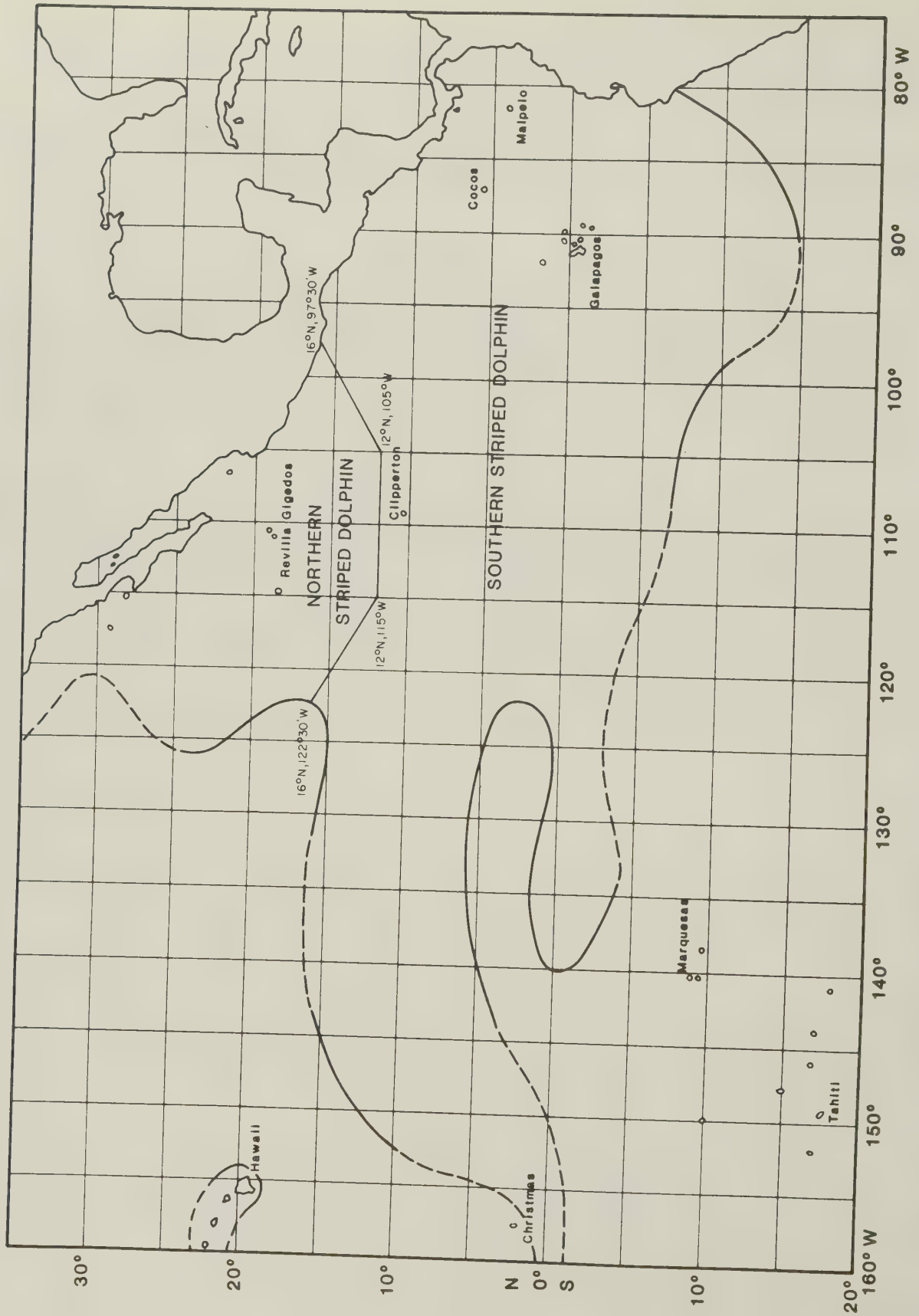

Figure 25. Recommended management units for S. coeruleoalba.

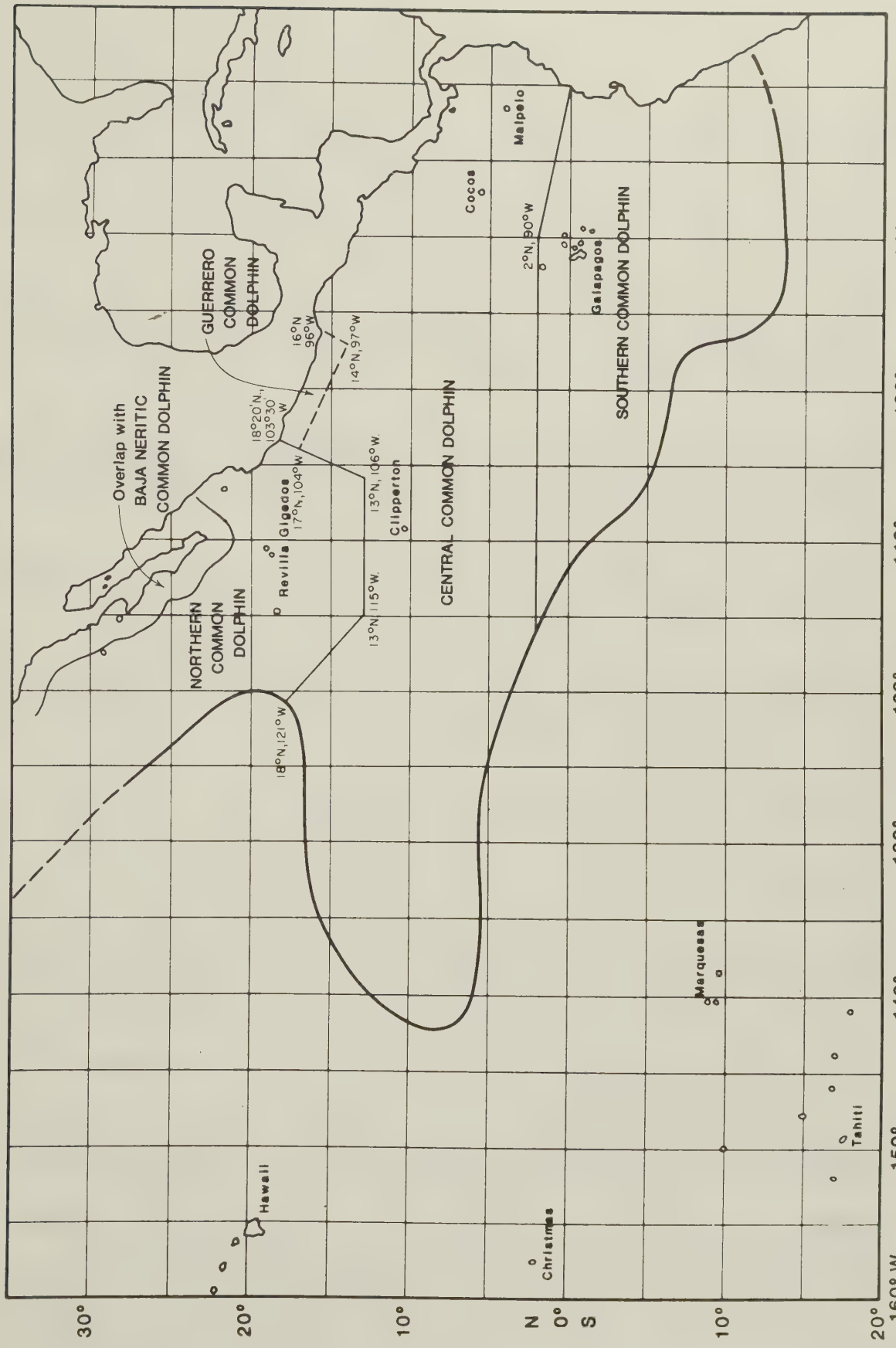

Figure 26. Recommended management units for Delphinus delphis in the eastern tropical Pacific.

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APPENDIX 1

Definition and Discussion of Population Terms

Stocks have been defined in a number of ways to fit different management schemes. For the purposes of this paper, a population or genetic stock is a single breeding unit characterized by relatively high gene flow within the unit and relatively low gene flow with adjacent units. The gene frequencies in one population will likely differ from those of other populations.

The population concept has been used successfully in management of other marine mammals. The fidelity shown by species of pinnipeds to particular breeding beaches allows populations to be identified and to be managed as such. Management becomes much more difficult, however, once these animals leave the breeding beaches for the open ocean. This approach has also been applied to coastal populations of bottlenose dolphins (Tursiops truncatus) affected by live-capture operations. Breeding units have been identified by long-term observations of marked individuals that occupied stable home ranges (Würsig 1978; Shane 1980; Asper and Odell 1980; Irvine, Scott, Wells and Kaufmann 1981).

Central to the definition of a population is the idea that gene flow is limited in some fashion between adjacent units. Restricted gene flow, however, may occur at several levels, making it difficult to identify what is a population and what is not. For example, discrete dolphin schools which are stable over time would subsequently have limited genetic exchange with other schools. Apparently such is the case for killer whales (Orcinus orca) which have been studied in Puget Sound (Balcomb, Boran and Heimlich 1982; Bigg 1982). Evans (1983) also presents evidence that members of common dolphin (Delphinus delphis) schools may differ morphologically from each other; thus the schools may be localized breeding populations.

Gene flow also may be restricted at the level of a herd composed of several schools. A group of schools which reside on a regular basis in the same area allows for more genetic interchange among these schools than with those occupying different core areas. This would be applicable to groups of schools which occupy overlapping, permanent home ranges, or whose movements are synchronized with each other. Coastal bottlenose dolphins have been found to occupy home ranges, in which membership of small traveling groups may change frequently while membership in the herd remains stable (Würsig 1978; Shane 1980; Asper and Odell 1980; Irvine et al. 1981).

A third level at which gene flow is limited is that of the geographical stock. Morphological differences among different forms is indicative of limited genetic exchange and found mainly in allopatric populations. Some gene flow might be expected, however, in areas of geographic overlap (e.g. eastern and whitebelly spinner dolphins) for highly mobile animals perhaps having complex social organizations, such as do the pelagic dolphins.

For the manager of pelagic dolphins, one problem in using strictly the population approach is the difficulty of identifying breeding populations of these wide-ranging animals. Another problem is that the size of identified population units may be so small, or the units so mobile, that assessments, monitoring and enforcement are prohibitive or impossible. The management unit, therefore, may encompass several populations (stocks) or portions of populations. For the management of large whales, the International Whaling Commission has defined a management unit as "a population unit most conveniently managed" (Allen, 1980). A similar definition has been used by the FAO Working Party on Marine Mammals (FAO, 1982). The emphasis of this definition is on practicality and ease of management. The actual breeding populations, however, may not be accurately assessed without supporting biological information.

The NMFS has identified ETP dolphin populations/stocks on the basis of morphological characteristics, apparent breaks in distributions, and oceanographic features (Smith, 1979), the approach used in this paper. The populations described by these criteria have been used in recommending proposed management units, which are defined largely on a geographical basis. This can sometimes be confusing, as research is conducted on the populations, while legal quotas are applied against the management units. Both the population units, defined as stocks for this and past NMFS reviews, and the management units have been revised over the years as new data became available.

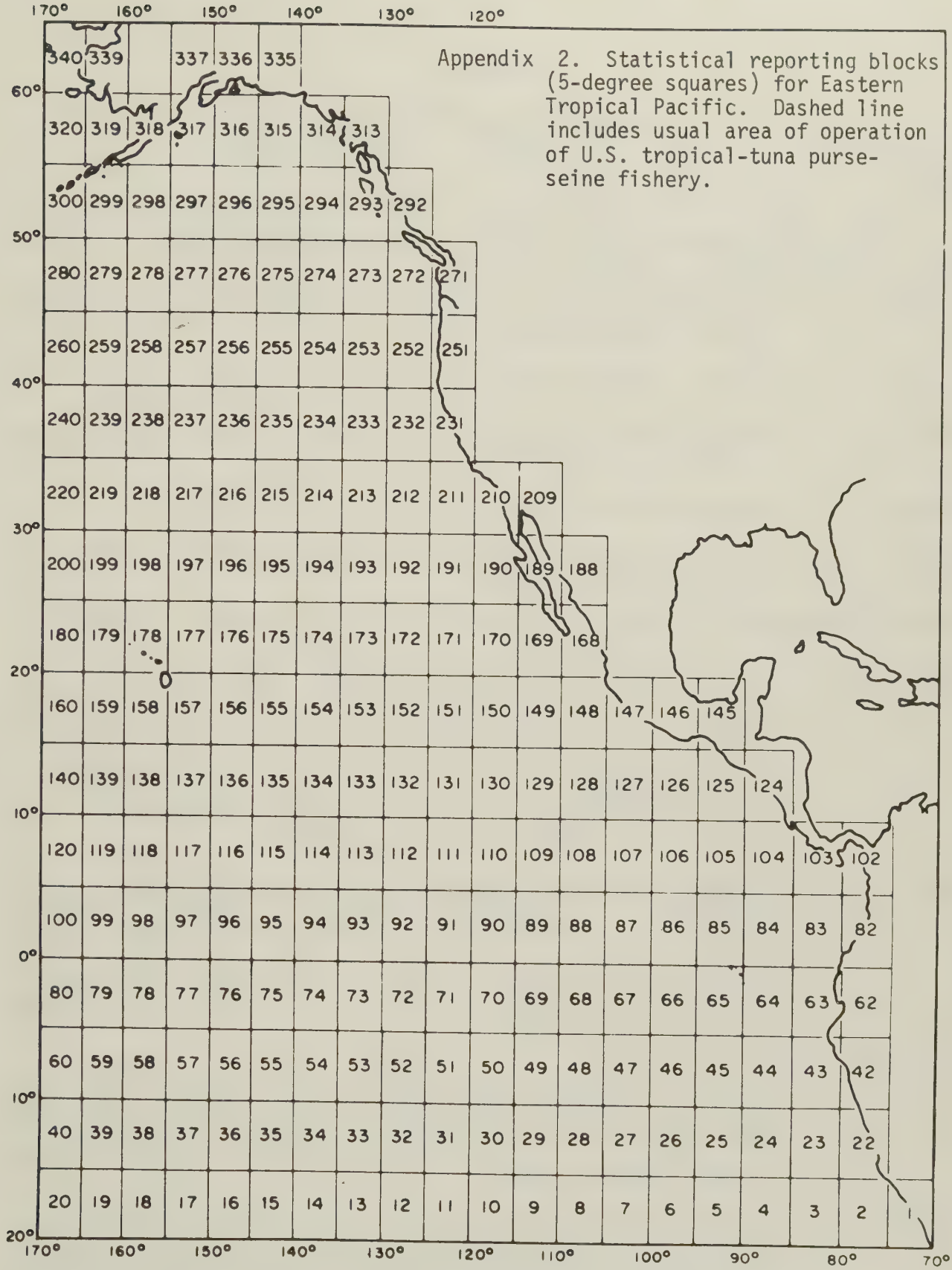
The IATTC recognizes those stocks which can be differentiated solely by morphological features or movement data (IATTC, 1980). This is a more population-oriented approach used for research purposes. The IATTC currently has no part in the management of dolphin populations in the ETP.

Other terms:

Subspecies - This is a taxonomic unit, indicated by a trinomial, and defined by Mayr (1969) as an "aggregate of phenotypically similar populations of a species, inhabiting a geographical subdivision of the range of a species, and differing taxonomically from other populations of the species. Mayr (1969) presents methods for determining how much difference in morphological characteristics is necessary before a species is divided into subspecies as opposed to genetic differences that are inherent in all populations. It should be noted that one cannot necessarily classify a single individual to one subspecies or another on the basis of morphological features since the ranges of variation of these features often overlap. The term race has often been used as a synonym for subspecies.

Form - This is a general term for referring to a morphological variant, the formal classification of which is uncertain.

School - The FAO Working Party on Marine Mammals defines a school as "a group of small cetaceans traveling together." Norris and Dohl (1980b) and Irvine et al. (1981) have used similar operational definitions in dolphin field studies.



Appendix 2. Statistical reporting blocks (5-degree squares) for Eastern Tropical Pacific. Dashed line includes usual area of operation of U.S. tropical-tuna purse-seine fishery.

APPENDIX 3

Computer Analysis of the Data

The computer systems set up to aid in the analysis of data for stocks involved five tasks:

Task 1 - Produce plots showing geographic distribution of stocks in the eastern tropical Pacific.

Task 2 - Identify outliers beyond the previous known stock range.

Task 3 - Show the comparative abundance of spinner dolphin stocks within a locality (i.e. a 5-degree square).

Task 4 - Determine the distance from shore for an animal.

Task 5 - Show the statistical distribution of body length by stock and sex for captured animals.

A brief description of each task follows (refer to the schematic diagrams):

Task 1 - For each stock, databases were created containing a subset of the data from the sighting database. The subset included cruise, date, sighting number, set number, species code and position. The Southwest Fisheries Center has a general plotting program called GPACK which utilizes a commercial plotting package called DISPLA. A slightly modified version of GPACK called GPACKP is used to produce the plots for this system using the modified sighting databases.

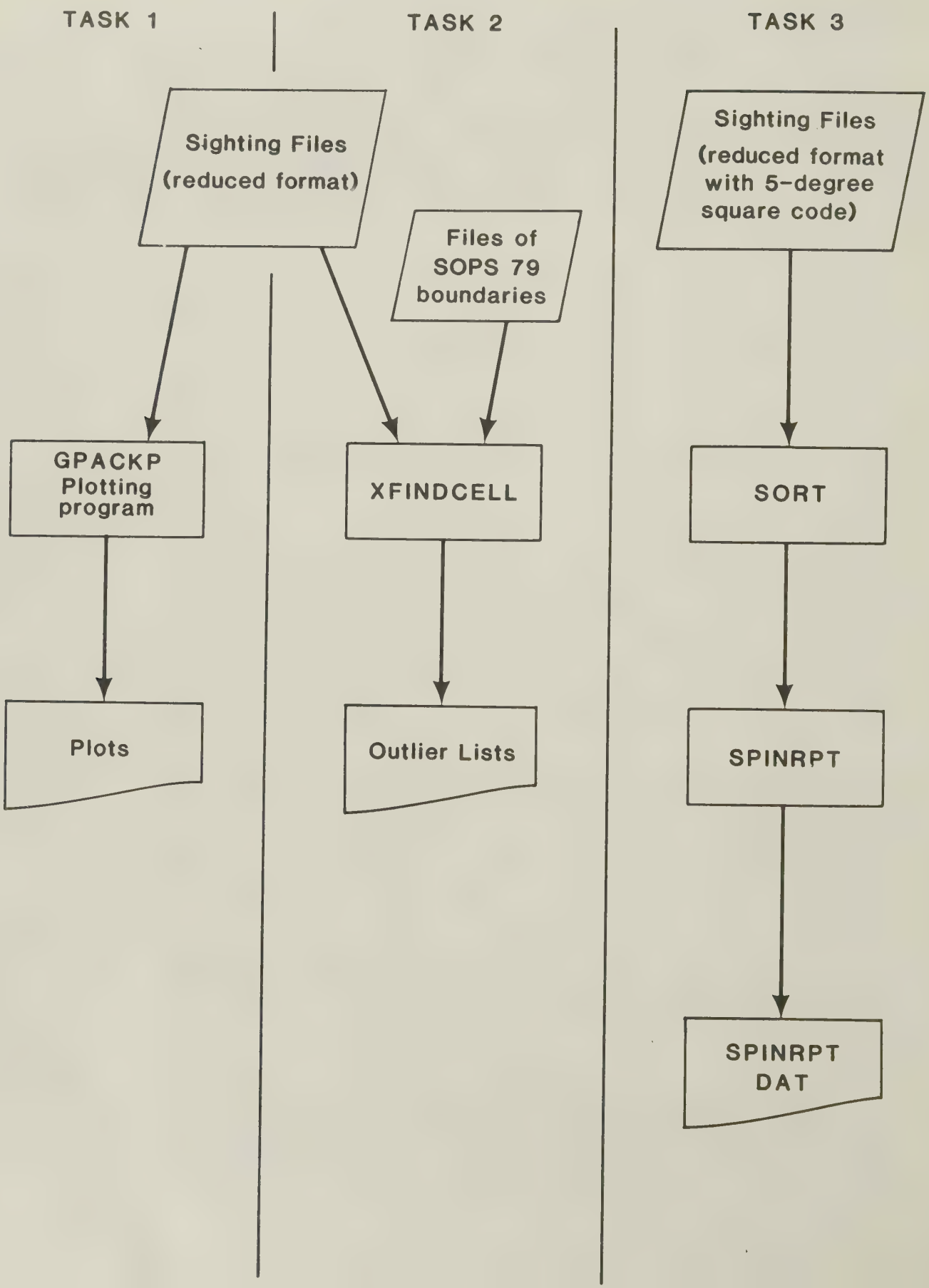
Task 2 - Southwest Fisheries Center has a program called FINDACELL which determines if a geographic position is located in a user-defined cell. XFINDCELL is a modification of FINDACELL which takes a polygon, in this case the SOPS '79 boundary for a species, and determines if a point, or sighting, lies inside or outside of the polygon. Points lying outside of the polygon are written to an outlier list.

Task 3 - A subroutine at Southwest Fisheries Center called SQR5POS can compute the 5-degree square code for each sighting. Ater this code is added to the sighting files, the program SPINRPT is run, which will list the counts and percents of spinner stocks in each 5-degree square.

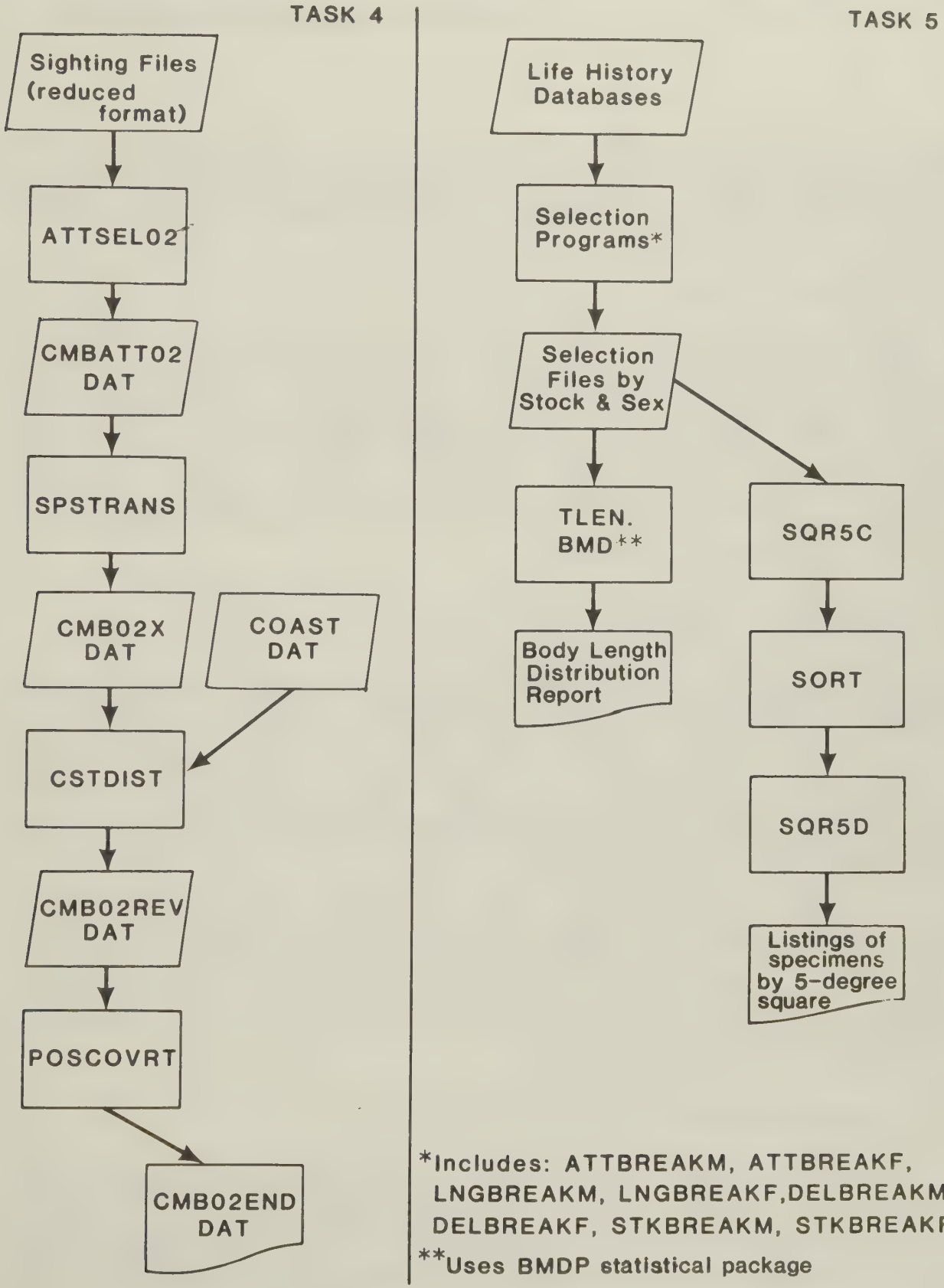
Task 4 - A system of four programs has been set up to compute the distance of a sighting from the coast. The computed distance is approximate and could be off by more than 5% in places where the coastline is highly irregular. Results were modified in cases where there were islands off the coast.

Task 5 - The data on body length for a stock is taken from the Life History databases. For each species-sex combination, a program is run to select only adult animals. These animals are grouped by stock. For each stock, the program TLEN.BMD is run which utilizes the P2D program from the BMDP statistical package. A summary report of body length distribution is produced. This task also includes programs SQR5C and SQR5D which produce reference listings of the animals selected in each stock-sex grouping.

ANALYSIS OF SIGHTING DATA BY STOCK



ANALYSIS OF SIGHTING DATA BY STOCK



*Includes: ATTBREAKM, ATTBREAKF, LNGBREAKM, LNGBREAKF,DELBREAKM, DELBREAKF, STKBREAKM, STKBREAKF

**Uses BMDP statistical package

APPENDIX 4

Review of Additional Methods for Identifying Stocks of Pelagic Dolphins

Preliminary studies have been done to test the feasibility of other methods of stock identification. None of these methods, with the exception of the aerial photogrammetric method, have been used to identify animals to stock in the current analysis. They provide, however, avenues for future research.

A. Non-metrical analysis of morphology.

Perrin, Yablokov and Cass (1982) developed a series of nonmetric characters for skulls of Stenella spp. and scored several single-school samples of S. attenuata and two of S. longirostris. The results of this initial survey indicated that the approach may be useful for studying geographical population structure in dolphins. Yablokov, Perrin and Mina (in press) identified and eliminated characters correlated with age and sex and applied more sophisticated statistical techniques to the same data, again with promising results. This work is continuing under the auspices of the U.S. - U.S.S.R. Marine Mammal Project.

B. Mitochondrial DNA Analysis

The degree of relatedness among populations has been recently measured for several mammals with the use of mitochondrial DNA analyses (e.g., Lansman and Shade, 1979; Brown, 1980; Ferris, Brown, Davidson and Wilson, 1981; Ferris, Wilson and Brown, 1981). Mitochondrial DNA is maternally inherited and has rates of evolution that are 5 to 10 times faster than those of nuclear DNA (Brown, George and Wilson, 1979; Gray, 1982; and loc. cit.). Consequently, the genetic differences among populations are greatly magnified by this technique.

This method is currently being used at the SWFC to study tuna and dolphin species in the ETP (Dizon, Graves and Ferris, unpub. MS.). A restriction endonuclease is used to fragment the mitochondrial DNA into pieces of characteristic sizes, and the resulting pattern becomes apparent with the use of electrophoresis. The amount of similarity or differences between two individuals can then be calculated.

C. Chromosome Banding

Studies on G- and C- banding patterns in the chromosomes of Stenella spp. have been conducted by Worthen (1981) under contract to the SWFC. Worthen examined the karyotypes of four specimens of spotted dolphins, S. attenuata, and one spinner dolphin, S. longirostris, to test the feasibility for separating stocks with this technique. G-banding was found to be quite stable

among species of Stenella, while C-banding was found to vary between species and among individuals. This technique has not been pursued farther because it was found to be prohibitively expensive.

D. Parasites

The use of parasites as biological indicators of stock identity has been suggested for dolphin species in the eastern Pacific. Differences in parasite fauna have been found for different stocks of bottlenose dolphins, Tursiops truncatus (Walker, 1981), and common dolphins, Delphinus delphis (Walker and Cowan, 1981). A preliminary study by Dailey and Otto (1982) under contract to the SWFC suggested that parasites may be potentially useful as biological tags for striped dolphins, S. coeruleoalba, Pacific white-sided dolphins, Lagenorhynchus obliquidens, and common dolphins, Delphinus delphis. It is likely that differences in parasite loads reflect different populations' feeding habits, although Walker suggests that possible differences in natural mortality cannot be ruled out. If parasites are indicative of feeding habits, however, then the parasite fauna would be characteristic of feeding congregations but not necessarily of breeding populations.

E. Aerial Photogrammetry

Aerial photography with vertically-mounted, large-format cameras has allowed dolphins in the ETP to be measured remotely and in large numbers (Perryman, 1980; Scott, Perryman, Laake and Ralston, unpub. IATTC cruise report). Photographs suitable for photogrammetric analysis require sunny and calm weather (Beaufort 0-2), and accurate measurements of altitude and tilt. Geographical forms which differ in length can be discriminated with this method, particularly since large sample sizes can be obtained without capture of the dolphins.

A photographic study was conducted of dolphin species off the coast of Mexico by the IATTC to gather information on reproductive parameters (Scott et al., unpub. IATTC cruise report). Photographed schools of dolphins can be identified to stock from measurements of photographed animals, e.g. eastern and Costa Rican spinner dolphins have an average difference in adult length of approximately 30 cm, while coastal and northern offshore spotted dolphins differ in average length by about 20 cm.

APPENDIX 5. Stock composition of records of *S. longirostris* by 5-degree block (see APPENDIX 2 for locations).

Block No.	Costa Rican No.	Costa Rican % of ID'ed	Eastern No.	Eastern % of ID'ed	Whitebelly No.	Whitebelly % of ID'ed	Total identified	Unidentified No.	Unidentified % of total	Total
3	0	-	0	-	1	100	1	0	-	1
23	0	-	0	-	26	100	26	1	4	27
24	0	-	3	7	37	92	40	2	5	42
25	0	-	0	-	16	100	16	0	-	16
26	0	-	0	-	4	100	4	0	-	4
43	0	-	0	-	13	100	13	5	28	18
44	0	-	4	2	167	98	171	16	9	187
45	0	-	0	-	97	100	97	5	5	102
46	0	-	0	-	31	100	31	1	3	32
47	0	-	0	-	1	100	1	0	-	1
48	0	-	0	-	1	100	1	0	-	1
54	0	-	0	-	2	100	2	1	33	3
55	0	-	0	-	1	100	1	10	90	11
63	0	-	1	3	29	98	30	29	49	59
64	0	-	3	7	41	93	44	13	23	57
65	0	-	0	-	102	100	102	22	18	124
66	0	-	0	-	32	100	32	6	16	38
67	0	-	0	-	57	100	57	6	10	63
68	0	-	0	-	21	100	21	1	5	22
69	0	-	0	-	13	100	13	0	-	13
70	0	-	0	-	9	100	9	0	-	9
71	0	-	0	-	1	100	1	0	-	1
72	0	-	0	-	1	100	1	0	-	1
73	0	-	0	-	2	100	2	0	-	2
82	0	-	1	13	7	87	8	2	20	10
83	0	-	18	37	31	63	49	37	43	86
84	0	-	24	26	67	74	91	49	35	140
85	0	-	15	8	183	92	198	55	22	253
86	0	-	9	5	162	95	171	31	15	202
87	0	-	22	12	155	88	177	24	12	201
88	0	-	17	5	310	95	327	23	7	350
89	0	-	2	2	131	98	133	13	9	146
90	0	-	4	5	82	95	86	17	17	103
91	0	-	0	-	70	100	70	4	5	74
92	0	-	0	-	29	100	29	2	6	31
93	0	-	0	-	2	100	2	2	50	4
102	0	-	6	67	3	33	9	14	61	23
103	9	6	75	56	49	37	133	82	38	215
104	2	2	60	51	55	47	117	80	41	197
105	0	-	51	47	57	53	108	70	39	178
106	0	-	236	70	99	30	335	164	33	499
107	0	-	220	61	142	39	362	167	32	529

APPENDIX 5. Continued

Block No.	Costa Rican No.	Costa Rican % of ID'ed	Eastern No.	Eastern % of ID'ed	Whitebelly No.	Whitebelly % of ID'ed	Total identified	Unidentified No.	Unidentified % of total	Total
108	0	-	169	43	220	57	389	172	31	561
109	0	-	42	31	95	69	137	46	25	183
110	0	1	25	24	81	76	106	34	24	140
111	0	-	26	10	231	90	259	62	19	321
112	0	-	21	5	378	95	399	57	13	456
113	0	-	12	3	345	97	357	57	14	414
114	0	-	8	3	294	97	302	28	9	330
115	0	-	1	1	81	99	82	7	8	89
116	0	-	0	-	1	100	1	0	-	1
117	0	-	0	-	2	100	2	0	-	2
124	3	9	25	74	6	17	34	36	51	70
125	0	-	653	92	54	7	707	494	41	1201
126	0	-	789	91	74	9	863	294	25	1157
127	0	-	664	93	53	7	717	190	21	907
128	0	-	932	88	132	12	1064	297	22	1361
129	0	-	481	86	78	14	559	132	19	691
130	0	-	229	76	74	24	303	88	23	391
131	0	-	70	35	129	65	199	58	23	257
132	0	-	60	16	312	84	372	73	16	445
133	0	-	27	8	306	92	333	55	14	388
134	0	-	6	6	101	94	107	6	6	113
135	0	-	0	-	23	100	23	4	15	27
136	0	-	0	-	5	100	5	1	17	6
137	0	-	0	-	1	100	1	0	-	1
138	0	-	0	-	2	100	2	0	-	2
145	0	-	0	-	1	100	1	3	75	4
146	0	-	65	94	4	6	69	44	39	113
147	0	-	203	96	8	4	211	132	38	343
148	0	-	86	90	10	10	96	45	32	141
149	0	-	192	93	15	7	207	104	33	311
150	0	-	97	89	12	11	109	46	30	155
151	0	-	4	67	2	33	6	2	45	8
152	0	-	1	17	5	83	6	3	33	9
153	0	-	0	-	9	100	9	0	-	9
168	0	-	0	-	5	8	5	46	44	51
169	0	-	0	-	6	30	6	9	31	15
Total	14	0.1	5,659	50.7	5,496	49.3	11,169	3,579	24.1	14,748

APPENDIX 6. Osteological specimens collected by SWFC for review of geographical variation but not yet analyzed, as of March 1982, with status as of March 1983. Juveniles included. For S. coeruleoalba and Delphinus delphis, major museum holdings of prepared and available specimens also given.

A. Spotted and spinner dolphins.	S. attenuata	S. longirostris
1. North of equator and west of 110°W (western portion of ranges of n. offshore spotted and n. whitebelly spinner dolphins).	131 (28 in preparation at museums)	46 (22 in prep.)
2. South of equator (s. offshore spotted and s. whitebelly spinner dolphins).	56 (21 in prep.)	41 (0 in prep.)
3. North of equator between 0 and 5°N and east of 110°W. (region between n. and s. population centers).	33 (5 in prep.)	13 (9 in prep.)
4. North of 5°N and east of 110°W (core area of northern ranges).	79 (38 in prep.)	43 (41 in prep.)
Total	299 (92 in prep.)	143 (72 in prep.)

B. Striped and common dolphins.	S. coeruleoalba	Delphinus delphis
1. Northern (temperate and tropical) stocks.		
a. New material	24 (0 in prep.)	34 (16 in prep.) (includes Baja Neritic)
b. Museum holdings	32	382 (" ")
2. Central tropical stock.		
a. New material	21 (2 in prep.)	97 (57 in prep.)
b. Museum holdings	46	252
3. Southern (temperate and tropical) stocks.		
a. New material	4 (in prep.)	0
b. Museum holdings	24	0
Total	151 (2 in prep. and 102 prepared)	765 (73 in prep. and 634 prepared)